EVOLUTION

(a Modern Synthesis)

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★ THEORIES

★ EVIDENCES

★ CAUSES

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Organic Evolution

Introduction

Even from very early days man began to explain away the origin of the world and the different species of living things existing on the surface of the earth. *The theory of Special creation* was commonly accepted. According to this all the living beings are creatures, created by an all powerful, self existing being called God. Representative animals and plants in all forms were created by Him in the beginning of the world. Later on some scientists brought forward the *Theory of evolution* or the theory of descent.

The term '*evolution*' is generally popularly considered atheistic in its essence. Its simplest meaning is *development* or unfolding. The theory of evolution tries to explain how the world and the various organisms found in it have evolved out of primitive beings. We can divide it into two main parts. 1. *Cosmic evolution*. 2. *Organic evolution*. Cosmic evolution tries to explain how from a nebulous mass the earth came into existence. *Organic evolution aims at showing that the various species of animals and plants extinct and existing today have descended genetically from one another through a graduated series of intermediate forms which link them together*. In simpler words, it tries to explain that the various organisms now present and extinct did not exist in the beginning of the world, life was then very simple represented by unicellular organisms out of which the various major animals have evolved in course of time.

The whole animal kingdom is considered to be one large family. The inter relationship of the various members can be expressed in the form of a genealogical tree. Similarly the plant kingdom can be explained. There is a missing link between cosmic evolution and organic evolution. How can inanimate matter produce living organisms? The theory of organic evolution does not

explain how life originated. Believers in God and evolution, '*Theistic evolutionists*' find here the necessity of the intervention of a supreme omnipotent and omniscient self existing Being. Some scientist propounded the theory of *spontaneous generation* or *Abiogenesis*. Even great scientists thought animals appeared from dead putrified matter. Even major animals like frogs and rats were thought to originate from moist soil. But *Pasteur* (1822—95) by a series of masterly experiments proved that in all the commonly alleged instances of spontaneous generation life really originated from living germs. Some scientists while admitting that abiogenesis no longer occurs still cling to the belief that it took place then under conditions that exist no longer. But scientists regard the laws of nature as invariable, always producing the same effect under similar conditions. Conditions that exist no longer can be produced in our modern laboratories. Yet no scientist has so far succeeded in producing living being from dead matter.

[The words in Genesis (1st Book of Holy Bible) regarding the creation of the world are not to be taken in the literal meaning. The 'days' mentioned may be considered to be a long period of time The Catholic Church condemns as contrary to faith the theory of *materialistic evolution* held by *Haeckel* (1834—1940) and others, which ignores completely the existence of a personal God and claims that life in all its forms including man with his soul had developed under the operation of blind forces or causes But she does leave us free to hold either the theory of special creation or theistic evolution Theistic evolution states that *God* allowed some or all species to develop in course of time either from inanimate matter or from certain created plastic primitive stocks. The early Fathers of the church held the theory of special creation. But St. Augustine, St Gregory of Nyssa, St Basil and the theologians of the middle ages like St Thomas Aquinas found no difficulty in admitting theistic evolution. Many of the modern Christian writers hold this theory That shows that *Theistic* evolution is not inconsistent with the teachings of Christianity. *Darwin* himself is a *Theistic evolutionist*.]

Evidences of Evolution

Is evolution taking place now? The answer that scientists give is 'yes'. It is taking place so slowly that centuries are required to see completely transformed species. Fr. Wasman S J. is of opinion that evolution

cannot be proved on any wide scale until about 2000 years hence. The accumulated observations of such a long period is deemed necessary to solve the many difficulties. The span of life of a man is very small. But the Theory is not a mere speculation; it is based on good scientific facts already existing which we call *evidences*. These can be grouped into the following :— 1. Morphological evidence : (a) comparative anotomy. (b) Evidences from Rudimentary and vestigial organs 2. Embryological evidence. 3. Geographical distribution 4. The palaeontological evidence. 5. Evidence of the precipitation method of blood-test. 6. Evidence from breeding.

Morphological evidence

(*a*) *Comparative anatomy*: Scientists have tried to classify the various animals found in the world. The ordering and classification of the multiplicity of animals was not an easy task. Several systems have been tried. The present method modifies after Linnaeus is the most satisfactory one. The animals are arranged in kingdom, phylum, class, sub-class, order, sub order, family, genus and species. A glance at the table of classification shows how each one is so arranged as to suggest that the animals have a gradation of development.

Intermediate forms between clear cut genera are also seen which serve as *connecting links*. Thus for example among the mammals very primitive forms such as the spiny Ant eater Echidna and the Australian Duck-mole exhibit characters of reptiles also. They lay eggs, possess a cloaca. These form a link between reptilia and mammalia and hence suggest that mammals have evolved out of repiles through intermediate forms.

Starting from *Amoeba* we can trace the gradual development of various systems and organs concerned with them in the more and more advanced animals. The Chordata are characterised by possession of a bony skeleton In the previous phyla there is no real skeleton.

Among the chordata in the various genera the development of this skeleton is very gradual. At first it starts as a small cartilaginous notochord in the tail region. If we can remove the brain of various forms of animal and place them side by side we can trace its gradual development from worms, insects, fishes amphibians, reptiles, mammals and man. In the mammals also we can find the gradual development of various systems in the various orders, the most developed is the highest form of Primates, man. His brain has large proportion of cerebrum with many sulci and fissures.

If we take the respiratory organs we find the lower animals are breathing with the skin. The arthropoda (insects) have tracheal respiration. Gill respiration is found in the lowest forms of chordata, the amphibians breathe with gills in their larval stage and slow transformation of primitive forms of lungs is seen in the adult stage. The reptiles no more breathe by gills, and the lungs are better developed in them. In the higher forms the lungs are well formed.

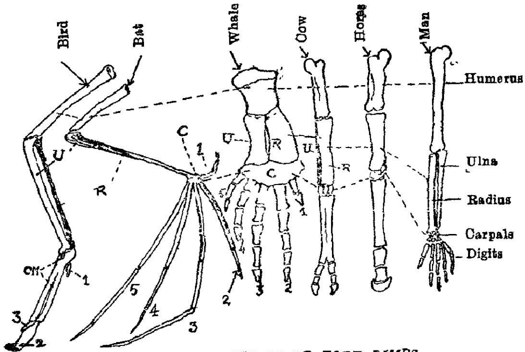
Among the chordata the heart shows a gradual development. In *Amphioxus*, in which the circulatory apparatus is so primitive, there is no heart at all. The ventral blood vessel which extends between the liver and gills is contractile and sends the blood forward. It is this part of the ventral aorta that makes the location of the future vertebrate heart. From such a primitive form the evolving heart passes through a series of modifications of increasing complexity until the four chambered mammalian heart is reached. (Amphioxus or Branchiostoma is the simplest known chordate animal, a 'fish in the making'. It is commonly called the 'lancelet')

The elasmobranchs and teleosts possess two chambered hearts. The amphibians have two auricles and one ventricle with one common outlet. The lower reptiles have imperfect four chambers and a common outlet in the alligators the four chambers are perfect and

the ventricles open separately into a branched vessel which is united at the bottom. The mammals have a more advanced heart with four chambers all having separate vessels connected with them.

The mouth parts of different kinds of insects afford good examples of modification of the same parts into cutters, suckers, piercing organ etc. This shows evolution within the order. The pentadactyl system of the limbs afford a good support for evolution among the chordates.

Though they exhibit a great diversity associated with the wide range of function they perform, like climbing trees, burrowing in the ground, swimming in water, jumping, flying, running, standing, striking; lifting and grasping and many other kinds of activity which call for particular modification of the type the vertebrate appendages are fundamentally built, on the same plan of structure. The fore limbs of a lizard, the wings of a bird and of a bat, the flipper of a whale or a seal, the fore legs of a horse or a dog are homologous with the human arm.



COMPARATIVE STUDY OF FORE LIMBS.

The paired appendages of the vertebrates above the fishes are built on the same plan having the same sequence of bones. It consists typically of a *girdle*, large shaft like bone called either the humerus or femur, two long bones, side by side either the radius and ulna or the tibia and fibula, a complex of several small bones making the wrist or ankle, a set of five long slender bones for the palm or the sole and lastly at the tips of each of the plam or sole bones, two, three or more small cylindrical bones forming the digits. Evolutionists consider that the animals referred to are the descendants of certain ancestral type having a similar plan of limb formation.

b. *The presence of Vestigial organ*: According to the evolutionists the vestigial or rudimentary organs are remnants or relics of organs which are disappearing due to disuse and they represent a part of group plan in ancestors to whom such organs in their developed form were useful. The nictitating membrane of the eyes of man is only a vestige which is developed and useful in the reptiles, amphibians, birds and mammals forming a third eyelid for protection. The small caecum with the vermiform appendix, the coccyx representing a much reduced tail, the hair on the chest and other parts of the body the muscles of the external ear which is useful in animals, the pineal body and many others make man a 'vertiable museum of antiquities'. Other animals too afford good examples of rudimentary organs. Some whales have rudimentary legs. Pythons and boas have a pelvis and rudimentary hind legs which are found near the vent not attached to the axial skeleton. This fact *reminds us of* the possibility of the descent of these animals from ancestors having well developed limbs. The stunted wing bones of ostriches, the very small stumps of wings hidden under feathers in the New Zealand Kiwi bird, the splint bones of the legs of horses repesenting lost digits are examples of vestiges.

FOSSILS

What are Fossils? DURING the earlier periods in the growth of geology as a science, and particularly during the Middle Ages, the word *fossil* (meaning anything 'dug up') was often applied indiscriminately to any curious object dug out of the rocks of the earth. These curiosities were thought to be 'devices of the Devil', 'irradiations' from the stars and planets, abortive attempts at creation, or mere freaks of nature. Yet many centuries before, some of the Greeks and Romans, who were not burdened with religious preconceptions as were the men of the Middle Ages, had correctly inferred that many of these objects were of organic origin. Even so, it was not until the middle of the eighteenth century that this fact came to be recognized universally and the term 'fossil' restricted to organic remains.

Definitions have inevitably varied from time to time. At the present day, however, fossils are regarded as the remains of plants or animals, or direct evidence of their existence, preserved in any formation of the earth's crust, irrespective of whether the sediment enclosing them is a hard consolidated rock or a soft incoherent deposit. It is clear from this definition that the impression of tracks made by animals, such as the footprints of dinosaurs, or of objects indicating the former presence of animals and plants, are as much fossils as the actual preserved remains.

There is a strong tendency to limit the word fossil to organic remains buried *before* modern times. Some people include within the term only organism fossilized before the beginning of 'historic' times, others restrict the term to remains fossilized before the end of Pleistocene times (see Table). These usages are not founded on any real difference in character between the remains buried before and the remains buried during the 'present' geological epoch. Indeed, there are many localities in the

world where fossil shells are weathered out on to modern beaches from Tertiary rocks tens of million years old, to occur side by side with, and to be practically indistinguishable from, living forms belonging to the same species.

Animals that have become extinct in historically recent times cannot be denied inclusion within the fossil category. Several flightless birds provide interesting examples. The well-known Dodo was a large pigeon-like bird formerly inhabiting Mauritius. It was exterminated by early settlers around 1681, and its remains are still found almost unaltered in peat bogs on the island, with even feathers and ligaments preserved. The giant Moa of New Zealand became extinct 500 to 700 years ago on North Island, soon after the arrival of the Moaris, but it lingered much longer on South Island. Numerous bones have been found in swamps and caves, some fragments from very dry caves still exhibiting ligaments, skin and feathers. The penguin-like Great Auk, which inhabited the North Atlantic, was another bird that had lost the power of flight; it was finally killed off by boat crews around the year 1844, but a few skins and eggs are still preserved. Other famous animals not long extinct are the so-called Irish Elk, the gigantic deer which lived in northern Europe in Pleistocene and prehistoric times; and the Sea-Cow, a large aquatic mammal formerly inhabiting the Bering Strait, which was exterminated by Russian sailors about 1768 and nearly complete skeletons of which have been found in superficial deposits near its old haunts.

However, extinction is not a criterion of fossilization; some species of molluscs found in rocks of Tertiary age still flourish at the present day. The idea of great antiquity usually associated with our conception of fossils, though appropriate for the organic remains of early geological time, is not valid in all cases. The view of one of the great pioneers of geology, Sir Archibald Geikie, that the term fossil is as applicable to the bones of a sheep buried under the gravelly flood deposit of a modern

Eras	*Periods and Systems*	*Approximate Age of Base of System in Millions of Years*	*Life*
CAINOZOIC (Time of Recent Life)	QUATERNARY: RECENT	Present Day	Modern Man
	QUATERNARY: PLEISTOCENE		
		1	
	TERTIARY: PLIOCENE	15	Origin of Man
	TERTIARY: MIOCENE	35	Rise of Mammals and Modern Flora
	TERTIARY: OLIGOCENE		
	TERTIARY: EOCENE	50	
		70	
MESOZOIC (Time of Middle Life)	CRETACEOUS		Age of Reptiles and Ammonites
	JURASSIC	120	
	TRIASSIC } NEW RED SANDSTONE	150	
		190	
PALÆOZOIC (Time of Ancient Life)	PERMIAN } NEW RED SANDSTONE	441	Age of Amphibians and Coal Measure forests
		220	
	CARBONIFEROUS	280	Age of Primitive Plants and Fishes
	DEVONIAN or OLD RED SANDSTONE	320	
	SILURIAN	350	Abundant marine invertebrates
	ORDOVICIAN	400	First appearance of life in abundance
	CAMBRIAN		
		500	
PRE-CAMBRIAN			*Rare* traces of soft-bodied life.
		1750+	
	ORIGIN OF THE EARTH	2000+	

THE GEOLOGICAL TIME SCALE

river as to extremely ancient organic remains, is the one now generally held though the limiting time in connection with the usage of the term fossil is largely subject to individual judgement.

The act of fossilization may, in a sense, be regarded merely as the transference of a very transient living 'present' or 'modern, fauna and flora into the sphere of dead and *past* life. This is studied by the palaeontologist (who is concerned with a series of forms in time) rather than by the biologist (who deals with living organisms in an extremely fleeting 'present'). Present life merges gradually into that of the geological past, though unfortunately many characters (such as colour, mode of life, song, etc) used by the biologist are usually not available to the palaeontologist. As Professor H L. Hawkins has so aptly remarked, zoology and botany are but the journalism - or the modern record of events - of palaeontology, just as geography is, in part, the journalism of geology. It is always possible to argue humorously about the status of a newly-chloroformed rabbit on a laboratory bench, or a dead sheep in a flood deposit. However, the futility of such arguments becomes apparent when one considers the remarkably amicable union of palaeontology and biology on the common ground where the two sciences meet. The various natural sciences certainly overlap; nevertheless, the palaeontologist never duplicates the work of the biologist or archaeologist, even though the lines of separation between their respective spheres are indefinite, owing to the difficulty of subdividing the essentially continuous process of the evolution of living things.

Palaeontology is by its nature a biological science, since fossils were living, active, growing organisms at one time and were associated together in faunas. The palaeontologist uses techniques that are dominantly biological, and studies the remains of once-living things that were subject to the same biological processes and controlled by the same biological 'laws' that are directing present-day life. In fact, the division between living

things and fossils, as between past geological epochs and the so-called 'recent' epoch, is merely a conventional and arbitrary one. The present is only a transient phase in an ever-changing panorama of life as well as of environment.

How are Fossils Preserved?

As a matter of convenience, it may be said that an organism may be called a fossil if it is dead and is or has been *buried*. The idea of burial by some natural agency is at least implied by most people using the term. Sir Albert Seward expressed the opinion that "the disinterred body of a cat is not in the strict sense a fossil, as it was buried by Man, not by Nature". The question that immediately arises out of this attitude, of course, is whether man should be regarded as a natural agent, as indeed he must be if considered in his true geological perspective. Nevertheless, burial – whether by man or nature – is a criterion that is closely connected with the way in which fossils are preserved, for the process of fossilization is simply one of burial in the first place, and preservation by some method afterwards.

The actual degree of preservation, which governs the mode of occurrence of animals and plants as fossils, is controlled by many factors, such as the nature of the organism itself, the material of which it is composed, its habitat and mode of life, the time and method of burial, the nature of the surrounding sediment, and the events that affect it after its burial. Once burial is achieved, fossilization takes place either by the checking of decomposition by the exclusion of air and percolating water, or by the replacement of suitable parts of the organism by some relatively durable substance. In the majority of cases fossilization appears to be fortuitous, since comparatively few of the countless numbers of organisms that flourished in the past have been preserved. Charles Darwin said that "the fossils in the earth's crust are collections made at hazard and at long intervals", or,

in the words, of his disciple T. H. Huxley, " the whole geological record is only the skimmings of the pot of life".

Preservation Intact

Usually organisms do not remain buried for long periods, without undergoing some chemical change. Soft tissues are exceptionally perishable, and the preservation of a complete organism is rare. However, a few instances are on record of the preservation of organisms in a virtually intact condition, and notable amonst these are the famous frozen mammoths of Siberia Though numerous discoveries of these wolly mammoths (*Elephas primigenius*) have been made, the best-known specimen is the one found by a Russian hunter near the Beresovka River in eastern Siberia in 1900. Despite the great age of the specimen — something like 25,000 years — the preservation was so perfect that even the flesh was intact; in fact, the trunk had been partly devoured by wolves at the time of the discovery, as the animal lay buried in frozen soil, while the contents of the stomach gave an indication of the food that had been eaten. The beast had a long coat of shaggy black hair with thick brown wool underneath, showing that it was adapted to a tundra or Arctic environment. The evidence of fractured limbs, clotted blood in the chest, and unswallowed grass between the jaws in all probability points to a violent death, possibly by falling into crevices. Besides similar specimens of the woolly mammoth, the woolly rhinoceros (*Rhinoceros tichorhinus*) is also found preserved in a frozen condition. However, these discoveries are unfortunately rare and the method of preservation is quite exceptional.

Nearly Perfect Preservation

There are many ways in which parts of organisms may be preserved in an almost perfect condition, and the nature of the material in which the organism is buried clearly plays an important role in the process of

fossilization. Perhaps one of the best examples of the prefect preservation of minute detail is provided by the insects, leaves and flowers of Oligocene age trapped in amber, the fossil resin exuded from a species of pine (*Pinus succinifera*). It engulfed the organisms and then solidified by the loss of its volatile constituents without damaging the fossils in any way. The preservation of structure is remarkably good; even the limbs, wings and antennae of minute insects may be studied in detail under the microscope. Only the external skeleton, however, has been preserved. Pieces of amber containing these fossils are common along the southern shores of the Baltic, and drifted fragments derived from that area occur as far as Norfolk and Suffolk in the British Isles.

Natural oil is another medium especially favourable for good preservation. In oil-impregnated soil in eastern Galicia, Poland, specimens of the extinct wooly rhinoceros have been found with fragments of skin and flesh intact. Even better known are the asphalt 'death-traps' of Rancho La Brea, near Los Angeles, California, where the remains of a great variety of Pleistocene animals have been discovered in conditions that suggest trapping in asphaltic pools. Carnivores constitute roughly 90 per cent of the animals, and include wolves and sabre-toothed tigers; the herbivores on which they preyed include bison, horses, ground-sloths, camels, antelopes and elephants. The partly-devoured carcasses in the tar offered excellent feeding grounds for the carnivores, and the struggles and cries of the animals already mired probably lured others to the trap. Vultures and other birds of prey were also attracted by the presence of live bait, only to be trapped in turn, thus giving a vivid picture of the death-struggles that occurred at Rancho La Brea in Pleistocene times. It is only the hard skeletal parts, however, that have survived more or less in their original condition. Hair, feathers, and other soft parts, and even the horny claws of mammals or the beaks and talons of birds, have been destroyed.

In south-western U. S. A. the bodies of ancient Indian cliff-dwellers are occasionally found mummified owing to the desiccating qualities of dry air, and rare discoveries have shown that animals may be mummified in a similar manner under comparable climatic conditions. Thus, in a dry cave in southern Patagonia, the remains of extinct ground-sloths (*Neomylodon*) were found with patches of the hide intact, showing the presence of nodules of bone in the deeper portions of the skin and of shaggy reddishbrown hair on the outside. Some dinosaur 'mummies' of Cretaceous age are also known; in these, the drying of the scaly skin took place prior to burial, so that its surface was preserved as a perfect impression or natural mould in the surrounding sediment even though the skin itself eventually perished.

The external skeletons of many groups of animals, and particularly the shells of lobsters, crabs and other arthropods, contain chitin, a complex organic substance. Despite its fragile nature it is very resistant to chemical change and may thus be preserved in a virtually perfect condition through long periods of time, as is shown by the remains of 'sea-scorpions' or Curypterids of Silurian age from the Isle of Oesel in the Baltic. The chitinous skeletons of the extinct colonial marine animals called graptolites which flourished in the seas of Lower Palaeozoic times, are also occasionally found solid and intact in calcareous deposits. It is often possible toextract them from the surrounding matrix by means of hydrofluoric acid, and to cut a continuous series of sections by means of a microtome in the usual biological manner.

Isolated teeth and scales frequently occur in ancient rocks in an almost unaltered condition, and may persist long after the disappearance of the rest of the animals. The reason for this is that the teeth and scales of vertebrates contain a particularly high proportion of calcium

phosphate, a substance that makes them highly resistant and durable.

In the plant world, the tissues in most brown coals (lignites) appear to have undergone little change from the original state, except for the loss of water. The famous 'papercoal' of the Carboniferous of Tula, Russia, is composed of the stem-cuticles of gigantic club-mosses in a practically unchanged condition. In deposits dating from the last great Ice Age it is possible to find pieces of completely unaltered wood.

Unfortunately, colour is rarely preserved in fossils, but Palaeozoic and Mesozoic molluscs may occasionally show colour-banding. The pearly lustre or 'mother-of-pearl' of shells, though not produced by pigment, may still be seen in certain molluscs from Tertiary deposits such as the London Clay. However, in many fossils the filling of pores results in a darker colour, and on the whole it is true to say that the older the fossil, the darker its colour.

Traces of Soft Parts

The delicate and easily destructible softer parts of animals and plants are usually destroyed by rapid decomposition, but their *outlines* may be impressed on the surrounding sediment before they decay. Perfect impressions may be felt by plants, often showing in minute detail the venation of the leaves, despite the fact that the plant tissue has completely disappeared. The fine-grained Jurassic 'lithographic stone' of Solenhofen, Bavaria, contains even the impressions of the extremely tenuous wing-membranes of the flying reptiles called pterodactyls. Exceptional discoveries have also been made of the impressions of jellyfish, whose bodies consist mostly of water and are therefore very perishable. The radial canals and other structures are clearly visible in specimens of jellyfish of Middle Cambrian age from the famous Burgess shale of Mount Wapta, British Columbia, where

they form part of a remarkable assemblage including seaweeds, marine worms, sponges, sea-cucumbers, and soft-bodied crustaceans. Spectacular finds of this kind in rocks of Cambrain age are extremely rare and they serve to show that a wealth of soft-bodied forms probably inhabited the earth from very early times. One can only imagine the abundance of such life that existed in the past without leaving any trace.

Animal or vegetable tissue, being made up largely of carbon may be preserved as a black carbonaceous film, retaining the original outline of the organism perfectly despite compression. Coal Messure plants have generally been preserved in this way. The outlines of the soft fleshy parts of the aquatic reptiles (plesiosaurs and ichthyosaurs) of Jurassic times are often preserved as carbonaceoous films around the bones of the skeleton. The process, called carbonization or distillation is one of gradual loss of the volatile constituents and a relative increase in the percentage of carbon, leading to the formation of a coal-like substance. Coal itself is formed by the compression of masses of plant material, and usually retains spore-cases and other plant remains; it is produced by the same process of gradual loss of volatiles.

Although the soft parts of an animal may have been completely destroyed during fossilization, deductions about their structure, often in great detail, may nevertheless be made from the remaining hard parts. For example, from the impressions left by muscles on the insides of bivalved shells, the nature of the internal musculature may be reconstructed. The bodily outline of a fossil vertebrate may in a similar manner be restored from characteristic muscle impression on the bones. The law of bilateral symmetry frequently makes the discovery of a complete skeleton unnecessary; a right limb may be restored if the left is known, while the missing parts of one skeleton may be reconstructed from fragments of another of identical type.

But, although traces of the soft parts of organisms are extremely valuable to the palaeontologist, it is normally the hard parts (such as shells, teeth, scales, bones and the bark of trees), which are capable of resisting the numerous agents of destruction, and are therefore best suited for preservation as fossils. If an animal does not possess a hard shell or skeleton, its chances of fossilization are greatly reduced. The larval stages of many animal groups were completely soft-bodied, and also very small, so that it is unlikely they will ever be found as fossils.

Petrifaction

Various events subsequent to burial influence the whole process of fossilization. Even hard shells and skeletons seldom remain in their original condition, but are often altered after safe burial. Buried hard parts generally undergo a process called petrifaction, which means 'turning into stone'. The term petrifaction is popularly applied to all varieties of fossils and quite commonly to inorganic objects coated with calcium carbonate from calcareous springs. These usages, however, are not strictly correct; not all fossils are petrified, while petrified inorganic objects are not fossils. In the process of petrifaction, the original substance of the fossil is gradually replaced by some other mineral matter, practically molecule by molecule. This delicate process may preserve microscopic structure as well as the external form of the original fossil. The replacing mineral may also fill up interstitial spaces, such as the cavities in bone, making the fossil heavier and more compact.

Examples of the petrifaction of hard parts are extremely numerous, and replacing minerals are correspondingly varied. Calcium carbonate is a common constituent of invertebrate shells and may be replaced by silica, one of the most stable minerals. Sponges and corals are often silicified in such a way as to produce perfect replicas or pseudomorphs of the original in

external form but not in detailed structure. Replacement by silica may also start from various centres on the shells of mollusca, producing an imperfect crystallization in rings (known as beekite structure) which may destroy the original ornament of the shells. Another common replacing mineral is pyrite, the golden-yellow sulphide of iron, which may often completely replace the skeletal elements of the extinct graptolites. In the case of sea-urchins or echinoids, it is well known that each plate making up the globular skeleton of the animal is a separate crystal of calcium carbonate. This arrangement is often preserved on fossilization, since fresh calcium carbonate is usually deposited in crystalline continuity with that of the original substance.

The woody tissues of plants may undergo petrifaction as perfectly as the hard parts of animals. In the famous Petrified Forest of Arizona the ground is strewn for miles with blocks of silicified wood in the form of agate or chalcedony. These tree trunks were carried by streams from the area in which they originally grew and later deposited in an ancient river delta, ultimately to form part of a Triassic sandstone. The softer sediment around the heavy petrified logs has since been removed by erosion, leaving them as remnants on the surface. In another petrified forest, that of Cerro Alto, Santa Cruz, Patagonia petrified cones of araucarian pines (related to the modern monkey-puzzle) are finely preserved in silica. They are found buried in volcanic ash, suggesting that an araucarian forest of Tertiary age was overwhelmed by volcanic activity.

Near Rhynie in north-east Scotland extremely primitive plants have been discovered preserved in silica in a peat bog of Devonian age, with the delicate structures preserved just as they were in life. The petrified tree-ferns (cycads) from the Jurassic rocks near Scarborough are rivalled only by the spectacular specimens from the Black Hills of South Dakota, in which the minutest structures are finely preserved. Botanically,

of course, petrifactions are valuable, since they allow the detailed anatomy of extinct plants to be examined under the microscope almost as perfectly as in sections of modern plants. Mineral matter may be precipitated from percolating solutions in the cells, and in the spaces between them, so delicately that cell walls are not infrequently preserved practically unchanged or only carbonized.

It will be obvious from this discussion of petrifaction that the composition of a fossil at the present time is no real indication of its original state. Quite often, in fact, the greater the geological age of an organism, the more mineralized it is likely to be.

Moulds and Casts

Even after safe burial in a sediment which has later solidified, a fossil may be completely dissolved by percolating water. Nevertheless, it may leave an impression of its outer surface in the encasing rock in the form of a *mould*. Vast numbers of fossils fall into this category, particularly many of the fossil shells preserved in sandstones of Ordovician age.

When Pompeii was buried beneath a heavy shower of volcanic ash during the eruption of Vesuvius in A.D. 79 many of the two thousand inhabitants and their animals were smothered with great suddenness. Subsequent decay of the flesh and sometimes of the skeletons left hollow external moulds in the volcanic deposit, which, when filled with plaster, yield perfect replicas (artificial casts) of the bodies of men and dogs.

After the decomposition of the soft parts the hollow shell of an invertebrate animal may be filled with sediment. If the shell matter is later removed by solution, the infilling is left as an *internal mould*, and it has impressed on its surface the counterpart of the internal surface of the shell, with muscle impressions and other features preserved in reversed relief. The empty

space between the external and internal moulds of invertebrate shells represents the cavity originally occupied by the shell itself, and if this is filled by the percolation of mineral matter, a natural *cast* of the shell results. The terminology is identical with that used in foundry practice: casts are filled in moulds. Where an internal mould does not exist, an external one, such as the impression of a footprint, may become filled with sedimentary material to produce a cast of the original. In fossils that have been petrified, details of microscopical dimensions may be preserved, but, in contrast, casts and moulds usually reflect structural features merely as impressions of surfaces; thus a cast of the brain of a mammal is a cast showing the outer membrane — the convolutions, though discernible superficially, are not preserved in depth.

The moulds of fragile objects like leaves remain in the sediment long after the leaf substance has totally disappeared, and are called impressions or incrustations. Plants growing near hot springs, or deposited in calcareous waters, frequently become encrusted with calcium carbonate in the form of tufa, which makes moulds of the plants before the decay.

The bark of trees is always fairly resistant to decay, whereas the pith readily disappears, leaving a cavity. This cavity may be filled with sand or mud before the plant is mutilated, to produce a pith-cast surrounded by the carbonized bark. Pith-casts of this sort are frequent in the Coal Measures; those in sand tend to retain their circular shape, while those in mud are more or less flattened by pressure The fossil trees of the famous Fossil Grove in Glasgow are undistorted sandstone casts.

Evidences of the Former Existence of Organisms

Even when the organisms themselves are not preserved, they may leave evidence of their former existence. The movement of animals across soft mud or sand results in tracks or trails in the sediment which

may be preserved if quickly covered by another layer of sediment. The fossil footprints of reptiles are especially abundant in rocks of Triassic age, and they may reveal much about the animals that produced them. Thus, from a study of the shape of the footprints, the distance between them, and other features, it is possible to assess the size and bodily proportions of the animal, the length of its stride, whether it was bipedal or quadrupedal, and how it walked. Tracks are sometimes found leading to the remains of an animal; a lobster preserved in the Solenhofen limestone has the impressions of its limbs leading to it, indicating how it crawled just before death after being stranded on a mud flat. The tracks of the more lowly crawling forms of life such as worms are frequently found, usually as long striated grooves. Obscure trails may also be made on the soft sediment beneath the surface of the water by fixed plants swinging in the sea-current, or by the dragging tentacles of jellyfish.

Many animals such as molluscs and worms, which bore or burrow into the sea floor or even into the shells of other animals, commonly have their burrows preserved with a filling of a different kind of sediment. The animals themselves may be fossilized in their living positions within their burrows.

Faecal pellets that have passed through the alimentary canal of an animal are known as coprolites. In the case of fishes and reptiles they may provide significant information about the food and the feeding habits of these animals. Parts of the animals that served as food are often identifiable within the coprolites, notably indigestible fish scales. Unfortunately, it is only rarely that the complete unvoided content of the alimentary canal is preserved as a mud cast, revealing in full the outline of that structure.

The flint implements and other artifacts made by primitive man may be included within the fossil category;

so also may the brilliantly executed cave-drawings on the walls of his caves, and, in a sense, the actual places in which he lived — for example, the lake-village of Glastonbury or even a city such as ill-fated Pompeii. However, the study of these usually falls within the province of the archaeologist, and they may be regarded as fossils only in the very broadest sense of the term.

Conditions of Deposition

The mode of preservation of fossils is capable of infinite variety due to local peculiarities of entombment. Fossilization is dependent not only on burial and the habitat of the organism, but also on the nature of the sediment in which the fossils are preserved and the actual conditions prevailing during burial.

(*a*) *Burial on Land*

The buffaloes which ones roamed the North American Great Plains were killed in large numbers by ruthless hunting, but few traces of them now remain because the carcasses were not buried. Dead organisms everywhere on earth are rapidly broken up into their inorganic elements when exposed to the weather, and even the most durable hard parts of organisms must be buried quickly in some protective material if they are to escape decomposition.

The habitat of the organism exercises a direct control over the kind of protective material in which it may be buried after its death. Terrestrial animals, for example, stand less chance of preservation than marine animals — if only because the deposition of sedimentary material conducive to burial is rarer on land and often depends on accidental circumstances. On land, vast forests may disappear leaving little trace, and representatives of a terrestrial flora are usually preserved only by being swept into lakes or rivers. Land animals also are preserved relatively rarely and stand the greatest chance of being fossilized in fresh-water deposits laid down in lakes, del-

tas or on coastal plains. Caves provide a special environment for fossilization; in them, the remains of the animals inhabiting the caves, or animals carried there as food, may be preserved in stalagmite (which is the layered deposit of calcium carbonate commonly occuring on the walls and floors of limestone caves). The fossilized remains of primitive man are normally found in such cave deposits, which are fortunately protected from the normal agents of erosion.

A large number of fossil terrestrial vertebrates are known, but the greatest interest is attached to discoveries of an exceptional nature. For example, no less than twenty-nine specimens of ***Iguanodon***, a large bipedal dinosaur, were unexpectedly discovered during mining in the Cretaceous infilling of fissures or ravines in the Coal Measures of Bernissart, near Mons, Belgium. The animals must have been overwhelmed by a sudden flood and their carcasses deposited in fine silt in the ravine together with other organic remains.

The Primates, possibly because of their arboreal habit, have left a scanty geological record. This may be related to a number of factors. The presence of leit mould on the forest floor would favour the rapid decay of bones; their mode of life in trees would enable the animals to avoid being caught in swamps; and further, owing to the increasing complexity of the brain, they were animals with some measure of intelligence, so that they were able to avoid such natural deathtraps. Their bones of course, were liable to be devoured by carnivores, leaving little trace; in fact, vertebrate bones are occasionally discovered bearing transverse furrows which represent the impressions of the chisel-like incisor teeth of rodents.

Small land vertebrates are poorly preserved. The reason for this seems to be that the bones of small animals are frail, and may be completely devoured by carnivores. A wolf will merely pick the bones of an antelope, but will completely consume a rabbit. The earliest known

birds were quite small, about the size of a crow, and are known from only two specimens (Plate 16); even these were preserved in an unique lagoonal environment, which will be described later. Some species of fossil insects are known from single specimens, and their scarcity appears to be due primarily to their minute size, as well as to the little attention given to them by palaeontologists.

On land, fossils are sometimes preserved under desert conditions, and extraordinary finds have been made. In particular, the discoveries made in 1923-4 by an American expedition in the Gobi Desert, Mongolia, were notable for the great scientific and popular interest aroused at that time. Several clutches of the eggs of a small horned dinosaur (*Protoceratops andrewsi*) - some even containing embryos — were discovered in a red desert sandstone of Cretaceous age. It is possible that they were buried by drifting sands too deeply to hatch. The bones of a small ostrich-like toothless dinosaur were actually found above one of the nests, suggesting that it fed on the eggs and had been overwhelmed by sand when raiding the nest. The region appears to have been a desert land surface for long aeons of geological time — perhaps ever since the Jurassic period.

Exceptional examples of preservation on land are also seen in fossils preserved in wind-borne loess, which is a fine, porous unconsolidated dust. Nine complete skeletons of a peccary (*platygonus*) - a hog-like creature - were discovered buried in loess deposits of Pleistocene age in north-west Kansas : All lay close together facing in one direction, suggesting that they had probably turned their backs to the dust storm which suffocated them. A fall of volcanic ash on land may also preserve organisms in a remarkable way. Several successive forests were obliterated by volcanic ash in what is now the Yellowstone National Park area of the U. S. A. Many trees were buried in the positions in which they grew, and have in recent times been re-exposed still in

those positions by natural erosion, but with the woody material completely petrified.

(*b*) *Burial in Marine Deposits*

The most favourable conditions for fossilization exist in the sea, where the remains of marine animals are constantly accumulating on the sea bottom. In sandy and muddy sediments which are laid down not far from the shore, rapid burial is prevalent, and in fact, animals living on a shallow subsiding sea floor are most favourably placed for entombment. The great variety of physical conditions and the distinctive types of sediments laid down in this so-called 'Belt of Variables' are reflected in the diversity of the fauna. Since invertebrates constitute most of this fauna, as a group they stand the best chance of fossilization. Equally prompt burial is possible in the deltas and estuaries of rivers; in these environments there is frequently an intermixture of fresh-water and marine organisms, and possibly some forms derived from the land.

The habit and mode of life of the organism, therefore is coupled closely with the burial factor, and the actual chances of preservation vary with the habitat. Provided no erosion takes place, massive coral reefs, glass sponges with their vase-like skeletons, oysters, etc., are usually fossilized *in situ*, while gregarious animals such as brachiopods and echinoids which live together in large numbers are often preserved as entire communities. On the other hand, floating wood, seeds or fruit are easily dispersed by rivers or by ocean currents, and may be fossilized far from their original habitat.

Rapid deposition is invariably favourable to fossilization. Many fossils (for example massive corals) may be trapped in their life positions without mutilation or crushing. However, with slow deposition of sediment, two things may happen, either the fossils tend to be damaged by wave action (for example, the corals may be rolled about on the sea floor), or, if conditions are quieter,

rich condensed deposits with very little sediment in relation to the bulk of the fossils are formed (for example 'bone-beds' abounding in vertebrate remains).

In marine deposits, an animal community is not always preserved as a unit. A swimming or floating population (nekton and plankton) may become mixed with a bottom-dwelling population (benthos) merely by the sinking of the skeletons of the dead animals to the sea floor. Animals are not always buried where they die; they may be carried away by currents for considerable distances and then redeposited, often mixed with inorganic material of the same size and weight.

The character of the sediment is of paramount importance. A sandy rock is porous, so that it is possible for the original fossil material to be dissolved away by percolating water. Nevertheless, the sealing down of the sand by an overlying impervious layer of clay, or the cementing together of the sand grains, serves to prevent the circulation of water. A calcareous rock or limestone is also porous, but unlike a sandstone it may form a good matrix for fossils; they are usually preserved in their original form but are difficult to extract. A shaly rock is fine-grained and impervious, so that the detailed structure of fossils may be perfectly preserved, though crushing tends to mar their completeness.

Exceptional conditions of fossilization occurred from time to time in the geological past; perhaps the most notable example is the fine-grained, cream-coloured Jurassic limestone of the Solenhofen, Eichstadt and Kelheim areas of Bavaria. The rock is remarkable for the variety and excellent state of preservation of its fossils. The limestone was deposited as a calcareous mud in shallow bays or lagoons where extensive mud flats were frequently exposed. Fishes, crustaceans and jellyfish were often standed on these flats, whilst land animals, such as small dinosaurs, were sometimes trapped

on the treacherous surface. The calcareous sediment was probably brought by off-shore winds; these carried numerous insects and larger animals too, since the flying membranes of pterodactyls and the delicate wings and tail feathers of the earliest known birds (*Archaeopteryx* and *Archaeornis*) are well preserved in the Solenhofen limestone. The wet mud flats provided the moisture which was quickly absorbed by each successive layer of dry mud and which held this fresh sediment in place. The ideal condition of rapid burial in a fine-grained sediment was thus achieved and the excellent preservation of soft parts was a natural consequence.

Distortion and Destruction

A plant or animal may be perfectly fossilized only to be grossly distorted and even destroyed by physical and chemical forces. Pressure due to the great weight of overlying sediment may flatten or distort the fossil, or an oblique, shearing movement brought about by various earth pressures may cause the rock enclosing the fossil to be cleaved so that the symmetry of the original fossil is destroyed, as in many trilobites from the ancient Cambrian rocks of North Wales, or brachiopods from rocks of Devonian age in Devon.

If there is no distortion due to pressure, the fossil may be dissolved away completely by percolating waters, sometimes leaving traces in the form of moulds, as we have seen. Moreover, a fossil may be recrystallized out of all recognition; the minute structure is first destroyed, then the external form gradually becomes more obscure until it is ultimately lost; the object is then quite unrecognizable as a relic of ancient life. This process of alternation and recrystallization is included within the term metamorphism, and it often occurs in zones of increasing intensity towards huge masses of granite, such as that underlying Skiddaw in the Lake District, where all the fossils would appear to have been obliterated in the highly altered rock zones nearest the granite. Finally sediments containing fossils may be weathered or eroded

away by any of the normal agents of denudation which together wear away the surface of the land; the organic remains which once existed are consequently lost.

Conclusion

The palaeontologist, therefore, unlike the botanist or zoologist, does not have an abundance of living things at his disposal, and in many cases has little knowledge of the soft parts of the organisms he studies. Only a small proportion of the organisms which existed at any one time in the past are likely to be preserved as fossils, and we have seen that even those organisms that *are* fossilized may subsequently be destroyed. It follows, too, that only a proportion of the fossils that have been preserved are accessible to man, or are likely to be discovered by him, since untold amounts of sediment lie concealed under the surface of the earth. Nevertheless, despite these handicaps, the palaeontologist is in the unique position of being able to study plants and animals in a time-sequence, and herein lies the essence of the value of fossils in geology.

All the major geological systems and their sub-divisions are based largely on the succession of various forms of life in time, so that fossils form a foundation — the documentary evidence — on which much of geological chronology is built. The time-concept is the very motif of geology. Every facet of the subject is concerned with history, or a sequence of events in time. And since palaeontology is our best means of determining *relative* time, it rises to the first rank amongst the manifold phases of geology. The procession of life through the ages is a fascinating chronicle commencing with the dawn of life in recognizable form and the first appearance of organisms as fossils.

"Fossils are nature's hieroglyphics They include the sum total of our actual documentary evidence of organic evolution". They also form the ABCD in which the biological history is written. Fossil is defined as "*any body* or traces of body of animal or plant, buried and preserved by

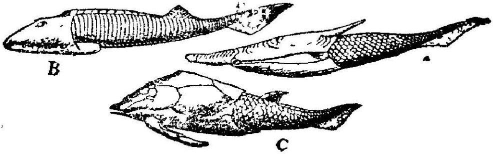


Fig. 1 Early Fishes with armour, (Restored from fossils)

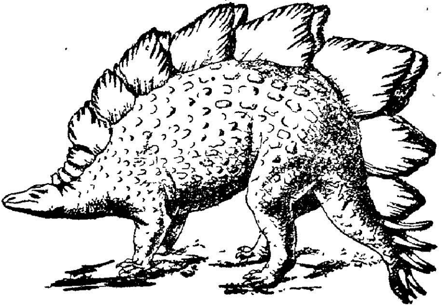


Fig. 2 STEGOSAURUS (An extinct giant reptile)

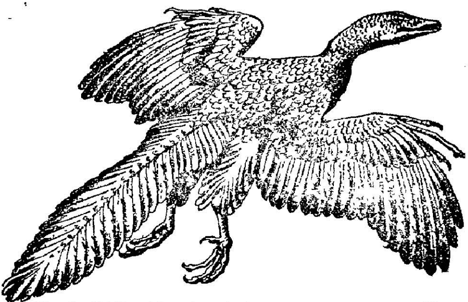


Fig 3 ARCHAEOPTERYX (Reconstructed from fossil)

natural causes". Every fossil is ancesstral to a living thing. It may also be representation of an *extinct* animal or plant. *Kinds of fossils:* Fossils may be [1] *Actual remains* of animals or plants such as insects buried in *amber* or the Russian mammoth in ice. *[2]* Minute *replacement* of the original organic matter by calcium salts or silica. This results in *petrifaction* (store formation). [3] Prints and impressions or moulds of the organism in coal, clay or gums of plants. [4] Preserved tracts, trails and burrows of past animals which are autographs of living animals.

Uses of fossils: [1] The study of fossils is called palaenotology. It forms an important evidence for evolution. See Palaeontological evidence). Fossils show the *Racial history* of animals and plants. eg. the history of horse is traced without serious gaps. [2] They are useful to indicate the past climatic conditions on the earth. [3] They also serve as measure of geologic time.

Palaeontological evidence: When available it is the final court of appeal. It is a proved fact that many more species of animals and plants were present in old times, and that many species are now extinct. We know of them only through the fossil remains that have been preserved in the various layers of rocks. *Fossils* are preserved animals or plants that existed long ago, or their parts either as they are, or replaced by Calcium or Silicon compounds. They are found between rocks or coal beds or in oil mines or ice as in Siberia. Geology is like a book, of which unfortunately many pages have been destroyed. However in the available portion a faithful record of all that has taken place in very ancient times has been kept. Some extinct species are known but many more have been recorded among lower strata. It is to be noted that all the extinct species mentioned in text books are only a record of the fossils which have been preserved, more or less entire, until now. But who could say how many millions more (perhaps also of unknown species and genera) have been lost or destroyed. The remaining fossil evidences show some connection in the transformation of one species into the other and hence form a proof of Evolution. *Archaeopteryx* for example is a fossil bird found in the Jurassic rocks. This shows teeth and many other reptilian features.

This is therefore a link between birds and reptiles. The evolution of *horse, elephant and camel* has been worked out in this way.

In the investigation of fossils from an evolutionary viewpoint, one of the early successes was Kowalevsky's account in 1874 of the *evolution of the horses*. Kowalevsky was able to study a series of fossil genera from the Old World. These he arranged in a linear series according to their geological age, and this series showed successive increases in size, reduction of the digits to a single functional toe, changes in skull proportions, and increases in the height and complexity of the teeth. Later studies have confirmed that the kinds of changes described by Kowalevsky did in fact take place, but in other ways have greatly altered the picture which he presented. Six genera are now known from the Old World (*Hyracotherium*, *Palaeotherium*, *Anchitherium*, *Hypohippus*, *Hipparion*, and *Equus* itself), which, if arranged in order of their appearance in the fossil record, do show more or less progressive changes in structure. But there are sharp discontinuities in structure between these genera, which might suggest that evolution had taken place in a series of jumps. That this is not so has been revealed by the study of fossil horses in the New World. It seems that although the surviving horse species are confined to the Old World, the major evolution of the group took place in the New, and that the Old World genera represent successive immigrations from North America at times when a land bridge connected Alaska with Siberia. From the New World fossils it is possible to reconstruct in great detail the evolutionary history of horses. It is known that the picture based only on Old World fossils is false in two respects. First, the apparent discontinuities in structure are no longer present when the New World fossils are taken into account. Second, the history of horses must be represented, not as a single linear series, but as a much-branched tree with many independent lines of decent. A simplified diagram of this history is shown in Figure. Only genera are repre-

sented as independent branches; if species also were included the picture would be vastly more complex.

The history of horses has been studied in greater detail than that of any other group. It is therefore worth considering this history further, and in particular to see how far it can be explained as a series of adaptive responses to natural selection. Changes in size, in the skull and teeth, and in the limbs, will be discussed in turn, although as will be seen the various changes are functionally related. Ref. Page 524 in Ekambaranathan.

A. *Size*: Modern horses are considerably larger than their Eocene ancestor, *Hyracotherium*. There has in fact been a general tendency towards greater size in a number of different lineages, but this has by no means been universal. Three quite independent lines showed marked decreases in size, and the existing wild horses are slightly smaller than their ancestors in the Pleistocene.

Nonetheless the commonest tendency has been towards greater size, and the same is true of other herbivorous groups, for example the cloven-hoofed mammals (Artiodactyls), the elephants (Proboscidea), and the herbivorous dinosaurs. The increase in size in some, but not all, carnivores can be explained as an adaptation to preying on the larger herbivores, but the causes of the increased size of the herbivores themselves are not obvious. It may in part be due to selection by predators. If at any given time the smaller individuals in a head are more likely to be attacked, this will select in favour of increased size. Another possible cause (first pointed out by Watson, whose argument has been slightly modified here) concerns the food requirements and thermal efficiency of heribivores. An animal requires 'fuel' to keep its body working, to keep itself warm (in mammals and birds) and to more itself from place to place. It has been shown that the energy required for these purposes is roughly proportional to the surface area and not to the volume of the animal: an animal twice the height requires four times as much food a day. Now

one of the factors which determine how much food a herbivore can eat during its lifetime is the time it takes for its teach to were down to the gum. Now, since the volume of tooth worn away will be proportional to the volume of food eaten, an animal twice as large, with teeth eight times the volume, will, other things being equal, be able to eat eight times as much food before its teeth wear our. Since it needs only four times as much food a day to keep itself going, its teeth should last twice as long. Thus increased size should, without any other change, increase the potential life span of an individual. It is interesting that those herbivores, mainly rodents, which have remained small, and which seek to escape from predators by burrowing, have grinding teeth which continue to grow from the root throughout life.

Probably there are other selective advantages in increased size in herbivores. For example, large browsing mammals can reach more food than small ones. Also, since the rate of utilization of food is proportional to the surface area, but the volume of food reserves in the form of fat is proportional to the volume, a large animal can go without food for longer periods. Nevertheless, as the history of horses shows, the tendency to increase in size is neither inevitable nor irreversible.

B. *Skull and Teeth.* Early on in horse evolution, during the Eocene, the premolars were modified so as to resemble the molar teeth, so forming a continuous and lengthened buttery of grinding check teeth, an easily understood adaptation. Further increase in the area of the grinding surface of the teeth could be achieved by increasing the length (parallel to the length of the jaw) of the individual teeth, and this in turn required a lengthening of the facial region of the skull to accommodate them. Such an increase in the length of the facial region of the skull is in fact characteristic of most horse lineages from the Oligocene onwards, leading to the familiar appearance of a horse's face. Robb has argued that the *relative* lengthening of the face may be a direct consequence of increased size. He has pointed out that

larger horses tend to have relatively longer faces, and that this is true whether comparison is made between the same individual at different stages of growth, between large and small adults of the same species, or between large (usually recent) and small (usually primitive) species. This suggests that the developmental pattern of all horses is such that the face grows relatively more rapidly than the body as a whole, so that an increase in size results in a change in skull proportions. If so, selection for increased size would itself also bring about a lengthening of the face. It is, however, important to remember that the changes in skull shape were themselves adaptive, and that if they had not been so, it is probable that natural selection would have altered the developmental relationship between size and shape.

Another important change in the teeth: in those species which adopted the grazing habit, there was a rapid increase in the relative height of the grinding teeth. In these same lines, but not in the browsing horse, there also developed a more complex pattern of ridges on the surface of the teeth. This is of importance in chopping grass into short lengths before swallowing it.

C. *Limbs*. The most important changes in the limbs of horses concern the mechanism of the feet. Early horses had feet functionally similar to those of a dog; there were four functional toes on the fore feet and three on the hind the weight being carried on soft pads. During the Oligocene one of the front toes was lost, but the padded condition remained. This type of foot was retained by all subsequent browsing horses. A dramatic change, well attested by fossils, occurred in the line ***Parahippus — Merychippus***, which was ancestral to all latter grazing horses. By a series of small, but, on an evolutionary time scale, rapid changes, a foot in which the padded digits lay flat on the ground evolved into one in which the weight when standing was carried on the

tip of the central toe. When additional weight fell on the foot when galloping, the central toe was bent forward, stretching elastic ligaments in the foot. The subsequent elastic recoil of these ligaments then helped to spring the animal off the ground at the next stride. The lateral toes were retained, and acted as buffers or stops preventing the ligaments from being overstretched. Finally in *Pliohippus* there evolved the foot mechanism found in modern horses; the lateral toes are reduced to vestiges, and their functional role as stops has been taken over by check ligaments in the foot.

The interest in this story lies in the fact that the changes did not occur gradually and continuously. Three functionally distinct types of foot, the three-toed padded foot, the three toed springing foot, and the one-toed springing foot, succeeded one another, each persisting for long periods with little change, and the transitions between them occurred rapidly in single lines of descent. Each type is probably an improvement, in a galloping mammal, on its predecessor. The rapidity of the transitions between them, however, suggests that intermediate types of foot mechanism would have a lower efficiency; consequently selection would act so as to preserve an existing mechanism, or once some threshold had been passed, rapidly to perfect a new one.

The main trends in horse evolution can reasonably be explained as adaptations to a herbivorous life, produced by natural selection. When a change of habits occurred among the grazing horses, this was accompanied by rapid changes in the structure of teeth and feet. In so far as a number of related lineages tend to undergo similar evolutionary changes, this is because groups of animals which have adopted similar ways of life are subjected to similar selection pressures.

The direction of evolutionary change is determined not only by the environment, but also by the present

structure and habits of the organism and the uses it makes of that environment. This is illustrated by the gaits of land vertebrates. The tetrapods are descended from fish which swam by lateral undulations of the body. Accordingly, all reptiles which run on four legs move their legs alternately, the right hind leg and left fore leg being forward when the left hind leg and right fore leg are back, and vice versa; these limb movements are assisted by sideways flexions of the body similar to those of fish. It follows that those reptiles which have achieved high speed by adopting a bipedal gait are runners; they move their hind legs alternately. Of these the most important were the extinct archosaurs, including the bipedal dinosaurs, and their descendants the birds. All birds which travel fast on the ground run; only some of the perching birds hop. In contrast, all bipedal mammals except man progress in a series of leaps (e. g. kangaroos, jerboas, elephant shrews, Cape jumping hares). All these forms have evolved from relatively small galloping mammals; the gallop is a gait unique to mammals, in which the hind legs tend to move together and in which the backbone is flexed in a vertical and not a lateral plane. The exception among bipedal mammals is man, descended from arboreal and not from galloping ancestors. This contrast between bipedal mammals and reptiles shows how the direction of evolutionary change depends on the structure and habits of the ancestral population.

When a reversal or change in the direction of evolution has occurred, it usually reflects a change in the environment in which the population lives, or perhaps more often a change in the methods of exploiting that environment. One of the most entertaining illustrations of reversal in evolution is afforded by the Proboscidea (elephants), and concerns the evolution of that unique structure, the elephant's trunk. Since the trunk contains no bone, direct evidence of its evolution is lacking, but its course and causes can be deduced from changes in the bony skull. Our knowledge of proboscidean evolution

depends largely on the work of Andrews, amplified by Osborn; the functional interpretation given of changes in the skull and teeth was suggested by Watson. (Ref. Page 545 Ekambaranathan Chordata for Evolution of the Elephant)

The Origins of Major Groups

By a major group of animals or plants we mean a large group of species all of which have certain characteristics in common, as do, for example, all mammals or all insects. Now if the lineages of all existing mammals could be traced back in time, they would ultimately converge into a single lineage, although, it does not follow that the individuals in this ancestral line possessed all the characteristics of modern mammals. It is, however, the events occurring in such an ancestral lineage and its immediate ancestors and descendants which are referred to by the term 'the origin of a major group'.

It follows that one can only judge retrospectively whether the changes occurring in a particular lineage contribute to the origin of a major group; they do so if the descendants of that lineage, by speciation and adaptive radiation, give rise to a large and varied group of animals. Thus the characteristic feature of a lineage ancestral to a major group is that there evolved within that lineage some character or group of characters which are of selective value for animals living in a variety of different ways in a wide range of environments. To use an engineering analogy, an 'invention' is made which subsequently proves to have a wide range of applications. An obvious example is afforded by the origin of the birds from the *archosaurs*. We are fortunate in having two fossils, *Archaeopteryx* and *Archaeornis*, intermediate between the archosaurs and modern birds. As far as their skeletons are concerned, these two animals are typical small bipedal archosaurs; if nothing else were known of them they would not easily be recognized as bird ancestors. But luckily impressions of their feathers can be made out. It

was the evolution of feathers in this group which ensured that it would leave such a large and varied assembly of descendant species.

Feathers can perform at least three major functions. Not only do they provide a light and rigid aerofoil section for the wings, but they also trap a layer of air over the surface of the body, which enables birds like gulls and ducks to swim on the surface of water, and, of more general importance, which helps to keep the body warm.

This example will help to explain one of the difficulties often encountered in explaining evolution in terms of natural selection. It often seems that a perfected organ, although efficient at performing its function, is far too complex to have arisen by one or a few mutations, and yet is such that any intermediate stage between the absence of the organ and its full development would be incapable of performing this function. Thus it is inconceivable that the flight feathers of a bird could have arisen by a single mutation, but the intermediate stages between a scale and a feather would be useless for flight. In this case the difficulty disappears once it is realized that during the early stages of the evolution of feathers, the latter were probably of selective advantage because they conserved heat, and only later did they become functional in flight.

The evolution of feathers was the decisive event in the origin of birds. This achievement was followed by many other changes improving the powers of flight, of which the most striking were the development of a great keel on the breast bone to support the flight muscles, and the reduction of the long feathered tail to a short fan.

The birds are characterized by this one unique feature, the possession of feathers, and it is very likely that these evolved once only in a single lineage. The story is different for mammals, which differ from reptiles in a whole complex of characters, of which the following are among the most important:

(a) Their method of locomotion. The elbows have been rotated backward and the knees forward so as to lie under the body, and the characteristic gait is the gallop, in which the legs are moved and the back bone is arched in a vertical plane, and not in a horizontal plane as in a lizard.

(b) Their teeth are replaced only once, and there is a 'division of labour' between incisors, canines, and molar teeth.

(c) The air passages from the nose are separated by a secondary bony palate from the food passage from the mouth, thus enabling an animal to breathe and chew at the same time.

(d) They have lost the original bony covering of the sides of the head, retaining only the cheek bone; consequently there is more room for the free play of the temporal muscles working the jaws.

(e) The lower jaw is formed from a single bone, the dentary, articulating directly with the side of the skull, while the two bones (quadrate and articular) which in reptiles form the jaw articulation, in mammals help to conduct sound impulses from the ear drum to the inner ear.

(f) They are warm-blooded, and covered with hair.

(g) They bring forth their young alive, the mother nourishing the unborn foetus through a placenta.

(h) After birth the young are fed on milk.

These various features did not all evolve at the same rate or time; in fact the living monotremes (*Platypus* and *Echidna*) still lay eggs and are primitive in some other respects. One or other feature may have been lost in some lineages; for example, bats are torpid when at rest, and whales do not gallop, although they still retain the arching movements of the backbone characteristic of small galloping mammals.

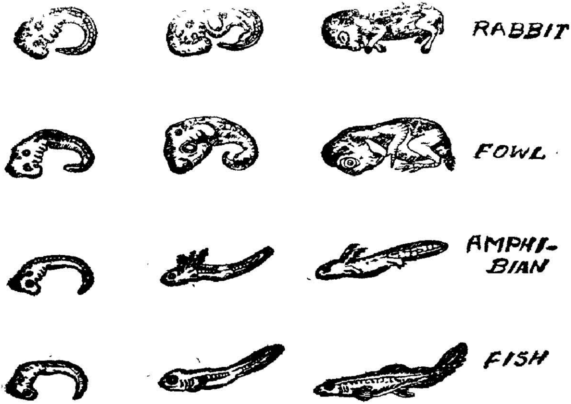
Little has been deduced from the fossil record about the evolution of the last three characteristics, but a good deal is known about the first five. One of the first great groups of reptiles to undergo an adaptive radiation were the 'mammal-like reptiles', which were the dominant land animals of the Permian, until they were eclipsed, but not wholly extinguished, by the archosaurs. Progressive changes in all these five features can be followed among these animals, from structures typical of primitive reptiles towards those typical of mammals.

The Evidence from Embryology

As a rule, only adult animals are found as fossils. Embryos and larval forms are small, and seldom have hard parts which will fossilize. Sometimes, particularly in molluscs, it is possible to deduce a good deal about the appearance of young individuals from the structure of adults, who carry around with them a permanent record of their shape when young. But it is in general true that the fossil record is a record of adult forms. Consequently the 'phylogeny' which can be deduced from fossils consists of a series of adults at successive stages in a line of descent. Each adult individual, however, was the end-product of a process of development; the development of an individual from fertilized egg to adult is called its 'ontogeny'. Thus although evolutionary changes are usually described in terms of the differences between successive adults, i. e. as phylogenetic changes the differences between those adults were the consequence of differences between the paths of development which gave rise to them, i. e. of ontogenetic changes; phylogenetic changes are the result of changes in ontogeny. It follows that a study of ontogeny, even though confirmed to living animals, can throw a good deal of light on the processes which in the past were responsible for phylogenetic change.

The task of describing accurately the ontogenies of animals was effectively started by von Bear. From his studies he drew some general conclusions. In particular,

be noted that the young stages of different animals often resembled one another more closely than did the respective adults. Later in development, an animal tends to depart more and more from the form of other animals. The early stages in the development of an animal do not resemble the adult forms of other animals, but tend to resemble the early stages of those animals. As we shall see there is much truth in these observations. A classic example is the resemblance between the early stages in the development of a bird and a mammal.



A COMPARATIVE STUDY OF THREE STAGES OF THE EMBRYOS.

After the general acceptance of evolutionary views by biologists, the resemblances between the ontogenies of different animals was given a new interpretation in Haeckel's 'law of recapitulation'. According to this view, an individual during its ontogeny goes through a series of forms resembling its adult ancestors; ontogeny recapitulates phylogeny. This has been expressed in the phrase 'each animal during its development climbs up its family

tree'. An example of the kind of evidence on which this view was based is the presence in the embryos of both birds and mammals of a series of gill pouches, not present in adults, although gill slits were present in the adult fish from which both birds and mammals are descended.

Unfortunately the facts do not support Haeckel, but suggest that Von Baer was right in suggesting that young stages resemble, not adult ancestors, but the young stages of those ancestors. For example, the gill pouches of an embryo mammal are much more like the gill pouches of an embryo fish than they are like the gill slits of an adult fish. Still clearer evidence is afforded by the presence in embryos of structures which could not possibly have existed in however modified a form, in any adult ancestor. Such are the extra-embryonic membranes, the amnion, allantois, and yolk sac, of developing birds, reptiles, and mammals. The evolution of the amnion and allantois was one of the decisive steps in the conquest of dry land by the vertebrates, since they serve to protect an embryo enclosed in a shelled egg on dry land, and enable it to respire. The allantois in reptiles and birds is a respiratory organ absorbing oxygen which has diffused through the shell; in placental mammals a derivative of the allantois contributes to the embryonic component of the placenta. These membranes therefore are embryonic adaptations. The resemblances between the extra-embryonic membranes of birds and mammals suggests that both groups are descended from a common reptilian ancestor which itself possessed such membranes as an embryo, but which certainly could not have possessed them as an adult.

The retention in evolution of the extra-embryonic membranes is explained by the fact that they have specific physiological functions to perform; without them, the embryo could not live, any more than an adult could live without lungs. But the embryos of birds and mammals resemble one another in the presence of a number of other structures which have no obvious physiological function to perform. For

example, embryo birds have a series of gill slits, and embryo mammals have gill pouches, similar in position to gill slits, but differing in that they end blindly and do not open at the surface of the embryo.

Thus related animals tend to resemble one another not only in adult structure but also in the mode of development of that structure. Sometimes the mode of development has proved more conservative, in an evolutionary sense, than has the adult form. For example, there is little resemblance in adult structure between flat-worms, annelids (segmented worms), and molluscs (snails, bi-valves, cephalopods). Yet some members of all these three phyla show the same pattern of cleavage of the fertilized egg into many cells, a pattern known as spiral cleavage. This pattern is so characteristic that it seems unlikely to have arisen independently more than once; it is therefore concluded that the three phyla are descended from a common ancestor.

It is often the case that those morphological features which are common to all members of a group are also the first to appear during development. In so far as this is true, it follows, as Von Baer noted, that the young stages of related animals resemble one another more closely than do the adults.

Every multicellular animal must undergo a process of development. Various methods of dividing what is originally a single cell into many cells, and of arranging these cells first into different layers and then into different organs, have been evolved. The methods of development of members of a given phylum usually have a good deal in common, the most obvious modifications being associated with differences in the size and yolk content of the fertilized egg and in the environment in which it develops. This persistence through long periods of time of a given method of development is presumably to be explained by the fact that any departure from the pattern proved less

efficient, and so was eliminated by selection. But any phylogenetic change in adult structure is the consequence of changes in ontogeny in successive generations. We must therefore consider the various ways in which ontogenetic changes can alter adult structure.

The various possibilities have been worked out by De Beer. Eight possible patterns of ontogenetic change are recognized.

In this list, the term embryo is intended to include free-living larvae also.

(i) *Caenogenesis*. The appearance during embryonic life of a new structure which in later phylogeny remains an embryonic structure.

(ii) *Deviation*. The appearance during embryonic life, and persistence into the adult, of a new structure.

(iii) *Reduction*. The appearance in the embryo only of a structure previously present in the adult, and the consequent reduction of the structure to a vestige in the adult.

(iv) *Neoteny*. The continuance of a structure, previously present only in the embryo, later and later in development, and finally its persistence in the adult.

(v) *Paedogenesis*. The earlier achievement of sexual maturity, and the consequent presence in the mature individual of structures previously confined to the embryo.

(vi) *Retardation*. The appearance of a structure at successively later stages of development, and its final complete elimination.

(vii) *Hypermorphosis*. The continuation of development beyond the stage reached in earlier ontogenies, and the consequent appearance of a new structure.

(viii) *Acceleration.* The appearance of a structure, previously persisting in the adult, at successively earlier stages of development, until it is confined to the embryonic stages.

Neoteny, Paedogenesis, and Retardation. The process of neoteny leads to the retention in the sexually mature adult of structures which were confined to the embryos of its ancestors. This can be brought about by the acceleration of the developmental processes leading to sexual maturity relative to other processes, so that maturity is reached in an individual which in other respects retains the characteristics of a larva. Alternatively, the rate of development of some one or few characteristics may be slowed down, so that they retain their larval condition in the adult. No sharp line of demarcation can be drawn between the former process (paedogenesis) and the latter (neoteny), and it is common to use the term neoteny to cover both.

Retardation is often merely another aspect of neoteny. If a larval character is retained in the adult, then the corresponding adult character of the ancestors will be lost in the descendants by retardation.

A classic example is provided by the axolotl a relative of newts and salamanders. Most newts have an aquatic tadpole stage, with gill slits and external gills, which, by a process of metamorphosis, is transformed into a mainly terrestrial lung-breathing adult. The laboratory axolotl normally becomes sexually mature without metamorphosis, retaining its external gills. It can, however, be induced to metamorphose by feeding thyroxin. The wild species from which the laboratory axolotl is probably derived normally undergoes metamorphosis. There are, however, neotenic populations in certain lakes in Mexico, but these differ in colour and in other ways from the laboratory axolotl, and should perhaps be regarded as belonging to a different species. The main interest of this example

of neoteny lies in the fact that a number of species of newts, for example the 'mud puppy' *Necturus* and the blind cave newt *Proteus*, never metamorphose, and cannot be induced to do so experimentally.

Hypermorphosis and Acceleration. As described in the last chapter, in large horses the length of the face in front of the eyes is relatively longer than in small ones, and this is true whether we compare adults of existing horses with adults of smaller fossil species, or the adult and young stages of the same individual. It follows that if, in the descendants of the small and primitive *Hyracotherium*, growth was continued to a greater size before maturity was reached, than the observed changes of skull shape in phylogeny would appear as a consequence of differential growth rates which seem to be common to all horses.

The phylogenetic change in the shapes of horses' skulls is an example of hypermorphosis; in this respect the young stages of existing horses do resemble their adult ancestors. Thus in cases of hypermorphosis, Haeckel's law of recapitulation is obeyed. In contrast, the changes in horses' limbs and teeth have been brought about by deviation during ontogeny; existing horses do not pass through a three-toed stage during development.

Evidences from Embryology

Although it is unwise to accept completely all the implications of Haeckel's hypothesis (*biogenesis*) yet the study of embryology, and particularly that of the higher Metazoa, does provide evidence of the existence of evolutionary processes. Every chordate, for example, commences life as a single cell, which, by division, produces a multicellular embryo These cells, by rearrangement into layers, by foldings and other varied alterations, give rise to a series of stages. In these the definitive structures are laid down, first in simple form, then by differentiation and growth becoming changed

and modified until the adult condition is attained. During this proces stages are reached which in their general organisation *resemble* those of definitive animals and the temptation to homologise these stages with adult animals proved too great for the Recapitulationists and direct comparisons were made. Thus the egg was stated to represent the protozoon stage, the gastrula the coelenterate and so on The ever increasing amount of work which has been, and is being, done on the development of animals has shown that many features manifested by the developmental stages are adaptations to particular conditions of the surroundings in which these stages find themselves. Thus, it would not be surprising to find that the embryological history of the frog which is passed through in water entirely apart from the body of the parent, is different from that of mammal which takes place in a specially modified part of the oviduct of the female. It is of extreme import, therefore, to find that, discounting differences which are clearly adaptational, the main features shown by the two types of embryo are very similar, and that the general sequence of events follows much the same course. In fact, there is a remarkable similarity between all early chordate embryos which is cogent evidence of their common orgin.

Other instances of this constancy of developmental ground plans could be cited, particoul arly in some parasitic Arthropoda, where the adults have lost almost all their arthropod characters, yet the constant appearance of characteristic larval forms (nauplius, cypris, etc.) enables the organism to be placed in its correct phylogenetic position.

Once again. the most telling examples have been found *within* different phyla (intra-phyletic), but the fact that is possible to discover some similarities of larval organisation between such widely different phyla (so far as adult organisation is concerned) as the Annelida and the Mollusca cannot be neglected as adducing evidence of relations *between* the phyla (inter-phyletic) So,

although it would not be wise to homologise the gastrula of a chordate such as Amphioxus or the frog with a coelenterate, since the embryo shows already the presence of chordate features, such as differentiated and potential mesodermal, notochordal and nervous cells and consequently cannot be said to be made up of ectoderm and endoderm alone as in the coelenterate grade of organisation, yet it is remarkable that there should be represented a stage, formed by the enclosure of certain cells (endoderm, mesoderm, etc.) within others (ectoderm) to produce a two-layered (but not necessarily two *germ* layered) condition. This condition, however, is probably related to the operation of similar physiological factors in the two cases.

It has already been emphasised when dealing with existing forms, that direct evolutionary relations between them are impossible to establish, and it is to the *stocks* from which they have arisen that reference must be made. Similarly, direct relations between existing embryological stages should not be sought, for they, too, have been subjected to the evolutionary processes; but if the presence of common features enables the detection of grades of embryonic architecture to be established, then this contributes to the conception that they represent an evolutionary series. In this view it is wrong to regard the mollusc larva as a modified annelid trochophore, but rather that these two larval forms both represent modifications of a common ancestral larva appropriate to the particular animal type to which they are going to give rise. (Here, again, exact knowledge is lacking, for, as in so many cases, no information of these ancestral larval forms is available.)

Another factor which has to be taken into account in the evaluation of embryological stages is that, just as the stages themselves have been modified, so also may the sequence of the stages be altered Phases may be telescoped, condensed or even omitted altogether so that the general picture is materially altered, yet the cropping

up of a feature here and another there may betray affinity. For instance, some Amphibia have become so terrestrial in habit that they do not return to the water to breed. Yet within the egg and before it hatches, a tadpole stage is passed through.

Again, the persistence of the appearance of the visceral clefts, (among other structures) in chordate embryos, even in those cases (e. g. mammals) where the majority of them never function at all and may not even be completely developed, their existence being merely transitory, is evidence of blood relationship with other vertebrates.

It suffices, therefore, if during the development of a complex metazoon the embryological stages show a series of grades of architecture of increasing complexity comparable to existing grades of orgnisation, then this is evidence for the operation of an evolutionary process and indicates the general trend that evolution has taken.

Evidences from Geographical Distribution

From the very large amount of informatian now available of the occurrence of the different kinds of animals in various parts of the earth's surface, it is clear that they are by no means evenly distributed. Not only have certain zones, determined by latitude, elevation, temperature, etc., their own characteristic faunas, but places with the same climatic conditions in different regions of the world do not always possess the same animal forms. Elephants, for example, occur in Africa and India but not in Brazil. The climatic conditions of the British Isles and of New Zealand are very alike, but the common animals in the two places are very different. Again, representatives of a group of animals may occur in widely separated places but not in the regions bet- ween them. The lung-fishes, (Dipnoi) for instance, are found in South America, Australia and Africa and nowhere else.

To explain the enigmas (riddles) of this geographical distribution, many suggestions have been put forward and valuable assistance from the fossil record has been forthcoming. The upshot of all these considerations is that different types of animals have frequently arisen in one area and then spread outwards, in radial fashion, in all directions and in many cases, the further they moved away from their place of origin the more they altered from the original. In such migrations limits are set by natural barriers. High mountain ranges, stretches of water, varying topographical and climatic features with correlated differences in vegetation and potential food supply, prevent the spread of purely land forms; differences in salinity and temperature, and currents and tides influence the distribution of aquatic forms. Aerial forms are less affected, their range corresponds to their powers of sustained flights. These barriers have by no means remained constant throughout geological time, for the configuration of the earth's surface has been altered by subsidences and upheavals. Land masses now completely separated by water were at one time linked up, enabling migration by land animals to take place.* In this way it has frequently happened that representatives of once widely distributed groups have become isolated in situations free from competition with more recent and highly evolved forms and have there survived. On the other hand, by the formation of new routes for migration, groups originating in a restricted area have spread to distant situations. Many animals (*e.g.* house fly, earthworn and whale) have become practically cosmopolitan.

Some of the most cogent evidence in support of evolution is obtained from the study of island faunas. Where islands have arisen by separation from a land

* Weyener's theory of continental drift, which postulates that the present continents were, originally a vast land mass in the southern hemisphere, which has become split up, and the constituent parts, have drifted apart has much to support.

mass, their faunas can be reasonably expected to resemble that of the neighbouring mainland and often do so, but almost invariably differences arise which can only be explained by the operation of evolutionary processes. Thus there is evidence that the vast island continent of Australia, was cut off before the eutherian mammals had achieved their present predominant position, and it is therefore of great import that almost all the mammals of that great continent are either monotremes or marsupials. Such native eutherian mammals as are represented like the dingo and rat, etc , have been introduced by man when he invaded these lands.

Again, the fauna of the British Isles affords an interesting example, because of its familiarity, of an island fauna of the so-called continental type. On the whole it may be said that the fauna of those regions nearest to the mainland approximates more closely to the continental than does that of districts more remote therefrom. In these more remote regions, too, the fauna is, on the whole, poorer in numbers of species. Thus snakes, common in eastern counties, are rarer in the west and are absent from Ireland. Many butterflies, rare or not represented in England, are common on the Continent. The small liver-fluke (*Dicrocoelum lanceolatum*) is fortunately absent from the British Isles though common in Europe. On the other hand, some species of birds, freshwater fishes and insects, though related to continental ones, are peculiar to these islands. Many other similar examples could be given.

It is also to be noted that the fauna (and flora) of the more easterly parts of the British Isles more closely resembles that of the west mainland, while that of south-west England and of southern Ireland shows resemblances to that of Mediterranean countries.

These facts can be explained when it is realised that during the Glacial Epoch the greater part of the

British Isles was submerged, with the consequent destruction of the animals and plants which at that time were *similar* to the *continental* ones. After a later re-elevation, the surviving forms on the Continent (to which England was still joined) migrated here, but this *migration* was *still incomplete* when partial re-subsidence took place with the separation, first of Ireland and then of Great Britain from the main land mass. From this *now* isolated fauna the present one has been derived with its marked peculiarities, similarities and differences from the continental one.

It is assumed, therefore, that the species which are peculiar to these islands must have *evolved* from the original fauna after separation from the mainland took place.

Instances of island faunas of a quite different kind are those of islands of volcanic origin which, when they first appeared were *devoid of land animal life.* Of such origin are the Galapagos islands, situated on the equator six hundred miles west of South America. Since it may be *presumed that when these islands* first arose above the surface of the sea as the result of some subterranean volcanic disturbance they would have no indigenous land animals, *then such as are now* found there must have come from the mainland either by flying, swimming, being carried by wind or ocean currents or *on driftwood or floating vegetation,* or introduced by man on his rare visits. Yet an examination of the animals has shown that although they bear some resemblances to those of the mainland, they clearly differ from them. In some cases, as the giant tortoises, they are peculiar to these islands and with the plants, some of the Galapagos species are not found elsewhere. Also, although the islands in the group are not separated from one another by very great distances, each individual island has its own particular species even among the birds. This condition of affairs is only explicable by postulating that after the species

from the mainland had arrived, they had undergone a process of evolution in quite different directions from those of their progenitors who remained behind, with tne production of entirely new species. It was the peculiarities of the fauna of these islands noticed by Darwin when he visited them in 1835 which influenced him in the elaboration of his views on evolution.

All these facts point to the conclusion that the present day distribution of animals is not completely explicable on the hypothesis of "suitability to environment." It is understandable, however, if two conditions are accepted; (I) that existing animals are the descendants of extinct populations which were of a more generalised type, and that these wandered out from their places of origin, (*becoming modified*) to meet the new conditions they encountered (adaptive evolution), intermediate populations possibly dying out; (2) that with the changes in the configuration of the land during geological time, certain groups became isolated due to the erection of barriers.

The Evidence from Comparative Physiology

All the facts so far brought forward in support of evolution have dealt with structural features; but it is clear that changes in structure *must* have been accompanied by corresponding physiological changes, and thus there must have been a physiological as well as a morphological side to evolution. All available evidence shows that, viewed as a whole, the physiology of the structurally simpler is usually less complex than that of the higher animals, and that animals said to be related to one another on structural grounds usually show physiological similarities. Direct evidence for an evolution of physiological processes from a simpler to a more complex condition is obviously unobtainable, but many interesting inferences can be made from present-day animals.

Evidence from many sources points to the view that the primitive members of most of the main phyla and

classes lived in the Palaeozoic seas or estuaries, and that only later did their landliving relatives become adapted to their new environment. The gradual transition, and some of the structural alterations which accompanied it in the vertebrates, have already been mentioned, but it may now be said that in their physiology even the most fully adapted of terrestrial vertebrates retain unmistakable traces of their descent from aquatic ancestors.

The analysis of the body fluids of both aquatic and terrestrial animals shows that they are fundamentally similar in composition and furthermore, that in their ionic composition they resemble sea water. Now the sea seems to provide a particularly suitable environment for most types of living organism and also has the merit of maintaining, within the rather narrow limits within which protoplasm can live, conditions which are fairly constant. A further point of interest in this connection is that the body fluids of most animals contain less magnesium but more potassium than does the water of our present-day oceans, but there is good reason for the belief that the sea of past geological time differed from modern sea water in a similar way. Higher animals have, as it were, retained the favourable features experienced by their remote ancestors during their life in the shallow seas which first formed on this planet.

In most of the simpler marine organisms the body is freely permeable and the body fluids automatically vary with changes in the surrounding sea water; but all vertebrates (and many other animals) are able to maintain the composition of their body fluids constant. This is a relatively easy matter for marine animals, but presents a greater problem for fresh water and terrestrial animals. Nevertheless, the problem has been solved by the development of excretory organs such as nephridia, Malpighian tubules or kidneys. These may be regarded from this point of view as having evolved to meet the need for maintaining a constancy of internal environment.

But true excretory organs have another important function; that of eliminating waste nitrogenous compounds from the body. It is interesting to find that it is characteristic of most aquatic animals that the bulk of the nitrogenous waste is in the form of ammonia; excess protein being merely de-aminated and the products not synthesised to form urea or uric acid. This is particularly true of the simpler invertebrates, but in amphibians urea is the chief excretory product. This difference is attributed to the fact that the very soluble but highly toxic substance, ammonia, must be rapidly eliminated from the body in dilute solution, and this is only possible in aquatic organisms. The elaboration of the innocuous substance, urea, from the ammonia released during de-amination, is a necessary complication of the excretory processes of land animals where the intake of water is of necessity restricted. In animals most fully adapted to life on dry land, *e. g.* the insects, reptiles and birds, the bulk of the excess nitrogen is excreted as uric acid or urates. These are practically insoluble substances, a property which favours absorption of water from the contents of the excretory tubules with the result that the "urine" is so concentrated as to be semi-solid, and a considerable economy in water is effected.

Thus it will be seen that an advancing complication in the physiology of excretion accompanies the structural complexity by which terrestrial ("higher") vertebrates are distinguished from the aquatic ("lower") vertebrates.

A similar correspondence between increasing morphological complexity and physiology has been found in the developing hen's "egg." The young embryo up to the fifth day excretes chiefly ammonia; from the fifth to ninth day, chiefly urea and from the ninth day onwards chiefly uric acid. Sometimes cited as chemical evidence for the theory of recapitulation, this instance is better regarded as an instance of developmental adaptation. The ammonia is produced in relatively small amounts

by the early embryo and to a large extent probably diffuses out through the shell. As time goes on the larger embryo, still confined within the shell produces greater quantities of nitrogenous waste and this is elaborated into substances which are less harmful. These can be passed out of the body, and because of their relative insolubility, stored in the allantois "out of harm's way." In any case, the urea is produced by a series of reactions quite different from those in fishes and Amphibia. At the most then, there is a parallelism between evolutionary and developmental changes in the nature of the substance excreted.

From what has been mentioned above it will have been gathered that the idea of homology between structures and organs in different kinds of animals implies that the evolution of new types has taken place by a series of small steps, the various parts of the animal body being altered almost imperceptibly in succeeding generations. The ground plan of the organ is always retained for long periods of time and evolutionary changes affect chiefly the details of structure. An organ or structure is not quickly discarded to be replaced by an entirely different one. Furthermore, structures must (with certain exceptions) at each stage of evolution have been of positive benefit to their possessors or they would have been eliminated. In just the same way animals have evolved physiologically, and much evidence for this can be found in a study of present-day animals. Innumerable examples of obvious similarities between the physiology of (structurally) related animals spring to the mind and all of these add weight to the view that animals took origin in common stocks. The probably universal occurrence of cytochrome in the cytoplasm of all aerobic organisms is a striking instance of chemical similarity between living matter and on a more restricted plane, but equally interesting, is the presence of the respiratory pigment, haemoglobin, in the red corpuscles of all vertebrates. The haemoglobin of different animals is not, however, identical for the protein component

differs and endows the pigment with different properties which can be seen to be adaptations to the oxygen needs of the body.

It has already been pointed out that the vertebrates are a particularly homogeneous group in the sense that the ground plan upon which their bodies are built is remarkably constant. Vertebrates are clearly related to certain of the protochordates (which are placed in the same phylum as the vertebrates), but links between these and the invertebrate phyla are obscure. The modern view, based largely upon embryological considerations, is that of all the non-chordates, the echinoderms are the most nearly related to the chordates. This theory received interesting support when it was discovered that creatine phosphoric acid, which plays an important part in the energy release for muscular contraction is found in the chordates and echinoderms alone, its place in the muscles of other non-chordates being taken by a similar but chemically different compound, arginine phosphoric acid.

Evidence from breeding experiments

The study of genetics has of recent years contributed much towards an understanding of how the small inheritable changes, which must have formed the basis of the evolution of one type of animal from another, have operated. In various animals which have been studied, both in the laboratory and in nature, it has been found that very occasionally one of a pair of allelomorphic genes may become altered in some way so that the character for which it is responsible is also altered. Such an inheritable variation from the parent stock is termed a mutation. Most of the mutations which have been studied have proved to be recessive and their effects are only evident in the homozygous condition, that is, when a recessive gene from both parents is present in the zygote. Mutations which behave in a dominant fashion are much rarer. Now it is clear that, owing to the rareness of a mutation in any animal population, the

chances are strongly in favour of an animal possessing the mutant gene to mate with one not possessing it; that is, with one of the normal type, so that if the mutation is truly recessive, the offspring, which are heterozygous for that character, will not show any change in body form. Hence selection will not begin to operate on the heterozygotes carrying the recessive mutant gene. On the other hand, dominant mutations, whether favourable or unfavourable to the species, immediately come under the action of selection and if favourable, the animals and their offspring showing the change tend to persist at the expense of the normal type.

In other instances where the mutant gene is not completely recessive but produces some effect in the heterozygous condition, it is found that if the mutation produces an unfavourable effect, then, by selection, those heterozygotes which, owing to differences in the gene complex manifest the least effect tend to persist, and after many generations the mutation therefore becomes completely recessive. The reverse effect takes place when favourable mutations occur. They tend to become dominant. Thus it is only to be expected that the bulk of the mutations which crop up in animals studied in the laboratory are both recessive and disadvantageous. They show themselves as departures from the normal or wild type of animal in which favourable mutations have been incorporated in the normal gene complex as dominant genes. There is, however, strong evidence for the belief that unfavourable recessive mutations identical with those observed in the laboratory occur also in nature.

It must be emphasised that selection in almost all instances acts on the effects produced by the gene complex as a whole, and only rarely on the effects produced by a single gene. Conversely, it is known that a single gene may influence more than one character. Certain of its effects may control definitely beneficial characters, but others may result in the

production of characters which are apparently of no benefit to an animal. It is in this way that many so-called non-adaptive characters may have arisen during evolution.

The actual cause of the mutational changes in the genes in nature is quite obscure, but experiments in which the chromosomes of *Drosophila* were subjected to the action of X-rays resulted in a vast increase in rate of mutation. Subjecting animals to the effects of different chemicals can also induce mutations. The behaviour of these induced mutations is in every way comparable to those which occur without any apparent stimulus. Whether or not these experiments have any real bearing on evolutionary processes occurring naturally is still uncertain; but the objection that all induced mutations are pathological has been answered by an experiment in which the subjection of mutant flies to the action of X-rays had the result of producing mutations in the reverse direction. That is, mutations were produced which caused the mutant characters to be replaced in the next generation by those of the normal or wild type.

A few instances are known of mutations of considerable magnitude by means of which a complete alteration of a species took place in a single generation. Many of the known instances were the result of a doubling or even of a trebling or quadrupling of the somatic chromosome number. Thus triploid, tetraploid and polyploid organisms are sometimes formed in one bound. This type of genetic change is really quite different from true mutations and clear-cut examples of it are known only among the plants. It is doubtful if it has played any significant part in evolution.

To sum up, the evidences from these six totally different sources, all tending in the same direction in supporting the concept of evolution, cannot fail in their accumulative effect to be impressive. It is impossible, therefore, without doing violence to the evidence to do otherwise than accept the *fact* of evolution.

APPENDIX I

Embryological Evidence (Contd.)

Difficulties of the Biogenetic law. Many biologists of Haeckel's time thought that embryology, when sufficiently known would be a golden key to problems of Phylogeny yet there was much unsound biology associated with the biogenetic law and few aspects of evolutionary science, have been so heavily attacked in recent years. The Recaptulation Theory assumes that embryos need only repeat the past condensing some stages, climinating others, without adaptation to the embryonic mode of life. Actually the embryo must cope with a hostile environment even as do adults. All pelagic larvae are subject to heavy predation. The first chapter in embryology texts frequently deals with differences in cleavage patterns which are correlated with amount of yolks in the eggs. Foetal membranes of amniotes are an obvious series of embryonic adaptations. Needham has described an interesting series of adaptations of eggs to fresh water, to salt water or to terresterial habitates. Each requires different excretory physiolgy and the last also requires a cleidoic egg. (encased in a shell) and other adaptations for water conservation. Thus mutations can affect embryonic as well as adult stages, and these too, are subject to natural selection, so that embryonic adaptations become part of the normal pattern of development.

The beautifully simple embryology of the echinoderms played an important role in the establishment of the biogenetic law. Yet the recent comprehensive study of echinoderm embryology by 'Fell' reveals extensive differences among various groups of echinoderms, and these differences are referable to embryonic adaptations. 'Fell' even casts doubt on the echinoderm-chordate relationship, for the hemi-chordate larva does not fit into the scheme of larval relation-

ships which he has worked out. Many biologists however feel that this is a result of extensive modifications of larvae by natural selection since the separation of their ancestors.

Another difficulty of the biogenetic law was Haeckel's emphasis upon resemblances of embryos to adult ancestors. Subsequent study has shown that the resemblance is primarily between embryos of related animals and only incidentally does this sometimes suggest adults. Thus ontogeny does recaptulate phylpgeny in a significant way, but it is ancestral embryonic, not adult, stages which are repeated and even these may be drastically modified by adaptive mutations which are favoured by natural selection.

Von Baer's Principles. In formulating his biogenetic law. Haeckel started from Von Baer's principles of embryonic differenciation and these are perhaps much sounder, a better guide to the embryolegical evidence for evolution.

These principles are the following:

1. General characters appear in development before special characters. 2 From the more general the less general and finally the special characters appear. 3. An animal during development departs progressively from the form of other animals. 4. Young stages of an animal are like young or embryonic stages of lower animals, but not like adults of those animals. The attack upon the Biogenetic law has never produced evidence that the findings of embryology do not support the facts of evolution. It has merely shown that Haeckel and his followers read into it more than the data will support. A return to the principles of von Baer makes possible a reasonable evolutionary interpretation of the facts of comparative embryology without straining the evidence.

APPENDIX 2

Evidences of Evolution.

From Comparative physiology and Biochemistry.

For more than three centuries before, Darwin, the great investigative impetus derived from the Renaissance resulted in the accumulation of a great store of biological Knowledge. On the whole it was a disorganised array of data, a burgeoning chaos, for there was no basic of the 'origin' caused a revolution in biological thinking because it provided just such a principle, a national frame work upon which the grand scope of biology could be organised. Its success in achieving this is one of the strong arguments for evolution. The biology of Darwin's time was almost morphological; physiology was in its infancy and biochemistry did not yet exist. Many biologists regard the morphological traits as simply the more obvious results of specific compounds and Processes. In short, they feel that evolution is basically a biochemical phenomenon. It is therefore significant that an array of very cogent evidence for evolution has emerged from these fields.

On the broadest level, there, is the fact that protoplasm appears to be basically one substance through out the living world. It contains very nearly the same elements compounded in to roughly the same proportions of proteins, carbohydrates, fats, water and supplementary substances. The functions of protoplasm are describable in most similar terms with few exceptions, through out the living world It is subject to other interpretations, but it strongly suggests community of origin, with the most fundamental properties of living things remaining rather constant, while variation in less essential respects has produced the immensely varied forms of the living world.

Much the same is the story with respect to the chemistry of the chromosome, the physical basis of heredity. It appears that, through out the entire living world the chromosomes consist of basic Proteins in combination with nucleic acid. Histone and protamine, which are the simplest type of proteins predominate, but globulin and some ~~incompletely identified~~ proteins are also present. The nucleic acids are also rather uniform. The basic unit of structure or nucleotide consists of phosphoric acid. Nucleic acids differ from one another in the base pairs which join together the nuclotide chains and much evidence now indicates that the specificity of the genes depends upon this trait also. In view of the great diversity of organisms it is astonishing that the chromosomes should have so uniform a constitution. But this is most readily under stood in the same light as is the general unity of protoplasm.

2 **Enyymes and Hormones.** Closely similar or identical enyymes and hormones are likely to be common to large groups of animals. Trypsin, the protein splitting enzyme is found in many groups of animals ranging from the protozoa to the Mammalia. Amylase the starch splitting enzyme is found from sponges to man. The thyroid hormone is also essential and found in all vertebrates. The pituitary hormone causes the pigmented cells of the skin to expand thus darkening the colours of the animal. It has no known effect in mammals. So this is a vestigial hormone.

Vertebrate hormones are variable. It has long been known that the pituitary growth hormone is not inter changeable among mammals. Beef hormone is not effective in treating deficiencies of this substance in children. Analysis of growth hormones, isolated and purified from various mammals, has revealed small but functionally significant differences comparable to the differences of structure with which comparative anatomy deals.

Haematological characteristics

If a drop of blood from a species having haemoglobin as its respiratory pigment is treated in the proper way, crystals of haematin can be obtained. The structure of the crystals differ from species to species and they parallel classification in a remarkable way. crystals obtained from all of the species of a genus share many characteristics while crystals from members of different classes have characterstics which are mutully exclusive. Thus it is possible on the basis of haematin crystals alone to distinguish between the various classes of vertebrates.

Comparative Serology. The most impressive physiologioal evidence is drawn from the field of comparative serology. If a small amount of the blood serum of any animal is injected in to a guinea pig, the foreign blood acts as an 'antigen' and causes the production in the serum of the guinea pig of antibodies which will precipitate and destroy the antigen, if a second inoculation should occur. The guinea pig is then said to be immunized to the kind of blood which was injected. Thus if one prepares an antiserum from an immunized animal and adds to it a few drops of antigenic serum a precipitate will be formed. This can be made by two principles. The first of these is the ring test method. A small quantity of undiluted antiserum is placed in a test tube and diluted antigenic serum is then carefully layered over it. A ring of precipitate forms at the interface between the two sera. If the two sera are mixed the precipitate will make the solution turbid and the photometric measurement of the absorption of light gives an excellent measurement of the strength of the reaction.

Such antigen — antibody reactions are highly specific. That is an antibody which precipitates the blood of one species is generally ineffective against the bloods of othor species. Yet the specificity is not

complete for serum immunized against the blood of any species 'A' will precipitste the blood of species related to A. For example, a guinea pig may be immunized with blood from the Common Salamder 'Necturus'.

If a sample serum from the immunized guinia pig is then divided among four test tubes; a few drops of serum may he added from necturus, amphiuma, Siren and cryptobranchus. The greatest precipitate occurs in the tube to which the necturus serum is added. Amphiuma and siren sera give about equal precipitates, while the cryptobranchus serum gives only a slight precipitate. On the basis of other criteria, it is generally agreed that the first three genera are closely related while cryptobranchus is a much more primitive Salamander.

Similarly, if serum from an animal immunized against human blood were divided among five tubes and serum added from man, an anthropoid ape, an old-world monkey, a new world monkey and a lemur, the amount of precipitate formed would also decrease in that order. Thus the results of serological tests. support the theories of relationship which were originally based upon camparative morphology. Thus it is exactly what would be expected on the basis of Darwin's theory that similar species have been formed by descent with modification from a common ancestor.

In general, serology has verified the taxonomy which was worked out in other basis, but in some cases serological data have been decisive in resolving difficult problems. Thus the King Crab Xiphosura was long regarded as a crustacean. Serological tests proved that it has little affinity with typical crustacean but with a spong affinity with Spiders. It was demonstrated that these animals share with spiders the fundamental arachinidan morphology. while their resemblance to crustaceans is a result of superficial convergence.

Blood Groups. The well known A. B. O, blood groups of man are based upon antigenic proteins of the red blood cells. Red cells may carry antigen A or B or both (AB) or neither (O), and a person's blood group is named accordingly. Any person's serum contains antibodies capable of agglutinating and destroying cells carrying those antigens not present in his own blood. Comparative series of blood groups have been found in many other animals, but only with other primates which are morphologically closest to man, does man share the A. B. O. Groups. Chimpanzees are predominently group 'A' but group 'O' also occurs among them. Gorillas and orang-utans are known to possess groups A, B and AB. In lower primates the same antigen proteins can be demonstrated in the saliva as in man but not on the blood cells. The inferance is that the relationship is unavoidable.

Biochemistry and recapitulation

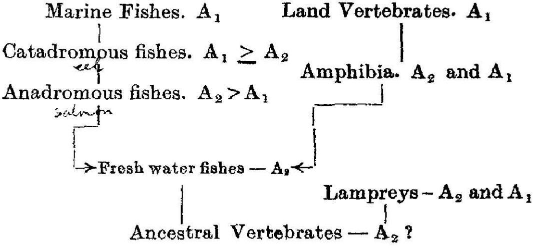
Phosphagens:— Few chapters in physiology have been so throughly investigated as muscle contraction. Energy - rich phosphate compounds play a key-role. Adenosine triphosphate (A T P) breaks down to yield energy for the contraction. Then a second energy-rich compound called phosphagen breaks down and realeases energy for the resynthesis of A T P. These reactions are anaerobic but the cycle is completed by the oxidation of glucose to provide energy for resynthesis of the phosphagen.

In the muscle of Vertebrates, the phosphagen is always a specific compound, creatine phosphate. The hemichordata has both phosphagens ie; Creatine phosphate which is found in invertebrates. Serological evidence affirms the relation-ship of echinoderms and protochordates, while failing to show relation-ship of the annelids to either of these groups.

Arginine and creatine are very closely related chemically and the former is actually used by vertebrates in the synthesis of the latter. In the embryos of sharks arginine is abundant but its occurrence in adults is more restricted. Thus it is possible that the creatine metabolism of vertebrates is a biochemical recapitulation comparable to the embryological recapitulations.

Visual Pigments. Vision among Vertebrates depends upon one or the other of two chemical systems in the rods of the retina. Fresh water fishes have visual purple, a porphyropsin — vitamin A_2 systems, while marine fishes and land vertebrates have visual red a rhodopsin — vitamin A_1 systems.

However some anadromous fishes like the Salmon live in the sea, but return to fresh water to breed. Anadromous fishes and amphibians are both hatched in fresh water and they undergo larval development. After metamorphosis, they migrate to salt water and to land respectively where they live much of their adult lives.



Actually tadpoles and young anadromous fishes have porphyropsin in their rods. At metamorphosis the morphological changes are accompanied by a change to a predominently rhodopsin visual system.

Later when the matture animal return to fresh water for breeding purpose they once again revert to a porphy ropsin systems. In catadromous fishes the facts are similar, but the sequence of changes is reversed.

On other grounds it had already been believed that the vertebrates originated in fresh water and there the ancestral fishes differenciated giving rise to fresh water and marine fishes and to amphibians. If this is correct, then the seguence of changes in visual pigments is best interpreted as a recapitulation — a condensed repetition of ancestral history. Similar facts have been worked out in amphibians for some aspects of blood physiology and excretary physiology. Thus it appears that the principle of recapitulution can give meaning to many otherwise inexplicable phenomena of bio-chemistry and physiology.

Wald has said that "without the rationalizations of phylogeny comparative bio-chemistry is little more than a catalogue." But evolutionary considerations do give meaning to this great and fundamental body of data, and this is cogent evidence for evolution.

APPENDIX

Catastrophism Versus Evolution

Before the time of Darwin it was customary to explain the facts of evolution by assuming that all life had been destroyed by catastrophes from time to time each catastrophe being followed by a new creation. As more and more paleontological information accumulated however it beame apparent that the number of catastrophes necessary to account for the known succession of floras and faunas was absurdly large and further that extinction of different contemporaneous groups was not simultaneous, as would be necessary under the theory of catastrophism. Under Darwin's theory it was not necessary to assume any catastrophes. Species simply changes continuously under the influence of natural Selection. The inevitable result is a changed aspect of the flora and fauna, fauna from one period to the next, with the difference increasing through out time. This does not require that the rate of change in different groups, or in different members of the same group, be the same.

Evolution of the Horse. Perhaps the most throughly known phylogeny of any vertebrate is that of the horse. The history of the horse, as understood to day covers a period of about 60,000,000 years beginning in the 'Eocene' period and involving twenty genera and a much larger number of species, although most of these are not believed to be in the direct line of descent. The oldest members of the superfamily Equoidea were the eight genera of the family paleotherridae, but these are usually not taken in to account in discussions of horse phylogeny, partly because of uncertainty regarding their relationship to more advanced equoids, but also because they show as much relationship or more to other mammals as to horses. Their "hooves"; for example, are quite claw - like.

The usual starting point of horse phylogenies is with " Hyracotherium ", the oldest known member of the family Equidae. This little animal stood less than a foot high at the shoulder and browsed in forest The teeth were forty four in number and the cheek teeth were only moderately specialised for grinding. The front feet had four toes and a splint, while the hind feet had three toes and five splints (representing the first and fifth toes). Yet already the third toe was more prominent, both front and rear than the other.

The line of descent appears to pass, with moderate changes at each step from Hyracotherium through Mesohippuss, Miohippus, Parahippus, Mery-chippus and Pliohippus to Equus, the horse of today and their allies. The changes achieved are great indeed. The size has increased from that of a house cat to that of the percheron. The cheek teeth originally low crowned and rather, primitive have become very high crowned and highly specialised for grinding course, siliceous grasses. These changes have been associated with elongations of the jaws and related parts of the head. The evolution of siliceous range grasses occurred simultaneously and probably served as a selective force acting upon the horses. The limits were elongated and simplified by the loss of some parts (legs) and the fusion of others (metacarpals and metatarsals). The neck became much longer and more mobile.

This phylogeny, emphasing as it does the six extinct genera believed to be in or near the direct line leading to living horses should not be interpreted as meaning that horse evolution has gone in a definite direction from the beginning, as though horses had from the first known where they were going and taken the more direct steps to get there. These many genera varied in several directions sharing some characleristics with their cousins in the " main line ", are differing from them in many others. Some line of

descent did not develop high crowned teeth. At every period in the evolution of the horse there have been widly varying genera and species. Natural selection has simply eliminated the great majority of these.

The validity of this series of horse fossils has been conceded by every one but some opponents of evolution have contended that the mere fact that such a series of genera existed in a succession from the most primitive to the most specialised does not require that the latter be descended from the former. They argue that each may have been independently created and that there is no reason why they should not have been created in an orderly sequence. There is no answer to this simply because it waives the evidence altogether. One could just as well say that there is no reason why they should have been created in particular sequence. It seems far more probable that the appearance of descent is there because the specialised horses actually are descended from the Primitive ones. But when one considers also the innumerable examples from all major groups of organisms which parallel the above case, the probablity that this appearance of descent is misleading, becomes very remote.

Evidence from genetics. The final line of evidence for evolution is drawn from genetics, the science of heredity. It may be stated however that it has been demonstrated that the genes are quite constant and are inherided on a statiscally predictable basis. They tend to keep species constant. However the genes are capable of undergoing a change (mutation) so that the one determined is different from the original and is just as stable. Hence mutation forms the basis of heredity, which is the raw material for evolution.

General topics for information

The Electron Microscope

The optical microscope seen in the laboratory has limitations in the study of very fine structure, because its effective magnification is limited to about two thousand times. It is true that we could magnify the image seen through the microscope many more times, but we should see no more detail the image would merely be larger. What is important in a microscope is power to resolve fine structure ie, to distinguish between points very close to gether—and it is this power of resolution which determines the clarity of the image which we see. An optical microscope can give clear resolution up to a magnification of two thousand times but no more.

In the early 1930's advances in our knowledge of electronics made it possible to design a microscope which uses a beam of electrons instead of light rays. The electrons are emitted from a tungsten filament and are accelerated by a high voltage. The beam is then concentrated and directed on the specimen to be studied. This specimen must be very small and thin (about .05 microns in thickness). As the electron beams passes through the object the electrons are scattered to a greater or lesser degree, according to the density of the regions through which they pass. Thus the electron beam which emerges from the specimen carries with it an image of the specimen. This electron beam is then diffracted as it passes through a number of carefully adjusted electro-magnetic 'lenses'. These are constructed of specially designed electro magnets which allow controlled deflection of the beam and so bring about magnification. Finally the beam is projected on to a fluorescent screen on which the pattern of electron densities becomes visible as an image.

In theory the principle of the electron microscope is fairly simple, but in practice there are many difficulties to be overcome. For instance the electron beam must pass through a vacuum and so all parts through which it passes including the specimen must be exhausted of air. There are many technical difficulties in the preparation of the object to be examined for it must be very thin ; and the operation of the microscope requires considerable skill and knowledge of electronics. The microscope costs thousands of pounds.

A more powerful electron microscope made has a resolving power which permits the user to distinguish two points 50 angstrom units apart and it is claimed that clear photagraphs 25,000 times larger than the part of the specimen examined can be obtained with this instrument. Even higher magnifications (half a million or more) have been abtained with the most recent instruments some of which can resolve points less than 10 angstrom units apart.

As a result of the invention of the electron microscope biologists are now entering a new era of discovery which promises to be as exciting as that which followed the invention of the optical microscope. It is too early to predict what discoveries may be made with the electron microscope, but we can be sure that by using it biologists will gain far greater insight in to the fundamental nature of living things.

LAMARCKISM

Lamarck. Jean Baptiste Lamarck (1744—1829) was born at Bazentin, in Picardy and was educated in a Jesuit College. In 1761 during the Seven years War he enterd the army, but was forced by poor health to leave it. Later he studied medicine and Botany. In 1788 Lamarck took a post at the Jardin des Plantes in Paris. In 1793 at the age of fifty he began to study Zoology. He invented the word 'Biology' to include the study of plants and animals. In 1809 he put forth his Theory of organic evolution.

His theory was based on two laws: (1) *The law of use and disuse.* (2) *The law of inheritance of acquired characters.*

The facts that animals and plants are adapted to the environment in which they live was recognised long before the theory of evolution had gained general acceptance among biologists. Similarly the idea that animals and plants could be classified according to a natural scheme preceded the idea that such a scheme suggested evolutionary relationships. It is infact the similarities and close affinities of the different species of animals and plants that led Darwin, Lamarck and others to an evolutionary explanation of the origin of species.

Lamarck was a pioneer exponent of evolutionary theory. He offered a theory which is "neither happily selected, nor convincingly put" so it was rejected by biologists and laymen alike. His evolution factor essentially consisted in his idea of use and disuse.

Adaptation in nature is quite a common fact. Examples can be given in hundreds to show that plants and animals adapt themselves to their environment. Rapid evolution is probably the result of the opening up of a new unfilled ecological or environmental opportunity. This may be because of the change in the organisation

itself for example when the birds develop the power of light. It may also be due to opening up of a new area as when a few fortunate colonists land in a new island or a condinent. One of the best examples of rapid changes is to be found in Galopages island that Darwin noted during his voyage. Darwin's finges are all descendants of a small number of chance migrants. They are a striking group in their adaptation to different feeding habits some have sparrow like beaks for seed feeding, others have a slender beak and they eat insect. The wood-pecker type is of special interest. It has evolved the habit of using a cactus spine in the place of the long tongue of the wood pecker (the only tool using bird), some finges have parrot like beaks and they feed on fruits. In the rest of the world finges are homogenous groups. A similar example of multiple adaptation is found in the honey creepers of Hawai, the long billed birds seek insects as wood-peckers do or nectar. The beaks of some are adapted to a diet of berries and seeds.

The inadequacy of Lamarckism :—

The philosopher Bergson and the french dramatist Moliere ridiculed Lamarckism. Nearly half a century ago Ray Lankester said, "Lamarckism is self contradictory since it maintains that a past of indefinite duration is powerless to control the present while the brief history of the present can readily control the future".

No need I go in detail through the wearisome discussion of the various sceintific proofs of Lamarckian inheritance that have been advanced says Julian Huxley; it would merely enough to say that subsequent work has either disproved or failed to confirm the great majority of them. Kammarers work on salamander (1924) has not been confirmed. Repetition Guyer's work on induced inheritance of immunity by other investigators has yielded only negative results. Some Lamarckians advance the view that the inherited effects of environmental modifications are so slight that

they cannot be described experimentally but require a cumulative action through thousands of generations to become obvious. But we need not pay attention to this view because exceedingly minute differences can be detected by proper technique. The total failure of sixty generation of disuse to affect the eye of Drosophila as shown by Payne 1911 is a good example of the failure of disuse to produce Lamarckian effects. An equally fundamental difficulty concerns all those innumerable cases in which the two sexes differ in adaptive character of structure and behaviour. For we know with certainity that the genetic constitution in the shape of chromosomes is distributed irrespective of sex. We find numerous cases of Lamarckian inheritance even if it existed elsewhere must be either impossible or exceedingly restricted.

The social Hymenoptera provide an interesting example. In them the bulk of work is done by neuter females. Reproduction is restricted to the full grown females, and males. How is it possible on any Lamarckian view to discover a mechanism by which the special instincts and structures of the workers have evolved. They cannot transmit them in reproduction for they cannot reproduce. Insects too offer many hard nuts for Lamarckians to crack. All higher insects emerge from the pupa into an adult or Imaga stage. During this stage they never moult and so they are incapable of local or total growth. Here again it seems all but impossible to imagine any mechanism by which any modification involving structural changes in hard parts could be transmitted.

These are some of most striking examples in which Lamarckian explanations cannot apply. Merely from the stand point of logic and theory most adaptation or functional evolutionary changes could be interpreted equally readily on the basis of indirect control by selection as on that of insect control by environment and use. We are therefore driven to ask why when numerous

adaptation are shown to be incapable of Lamarckian explanation we should postulate Lamarckism to account for others. Thus we are driven back to direct experimental proof, and that as we have already set forth is meagre and confusing. It is for these reasons that a good majority of biologists including the very great majority of those who have experience of actual genetic work repudiate Lamarckism or at least assign to it a subsidiary and un important role in Evolution. (Julian Huxley).

The Michurian trend of Heredity lays stress on the role of environment on the organism. Lysenko says "Heredity is the property of an organism to require certain conditions for its life and development and to respond in definite ways to various conditions."

Lysenko himself believes that if an organism is constantly put in changed conditions and in consequence develops along a different path, then at least in some cases its offspring also may tend to develop along the new path. This is the theory of Lamarck which has rather been called the inheritance of acquired characters. But there is no theoritical reason why the environmental conditions of the parents should not affect the nature of the progeny. It is in general true that striking changes can be produced in the phenotype of the individuals by changed conditions without affecting nature of the progeny. For eg. if two flies which have developed dumpy wings as a result of heat shock during their pupal life, are crossed their offsprings develop normal wings unless they too are supposed to have heat shock.

Two worlds — Two ideologies in Biology :- (Lysenko)

The Germ plasm theory which made its appearance at the turn of the century and Mendelism — Morganism which followed, were both primarly directed against the foundations of Darwinism.

Weismann made his conception of Neo-Darwinism but in fact it was a complete denial of Darwinism. The theory of evolution necessarily presupposes the recognition of hereditary transmission of individual characteristics acquired by the organism under definite conditions of its life. It is unthinkable without recognition of the inheritance of acquired characters. Weismann asserts that "not only is there no proof of such a form of heredity, but it is unconceivable theoritically". "Thus war was declared against Lamarck's principles of the direct transforming effect of use and disuse and indeed, that marked the beginning of the struggle which is going on to this day, the struggle between the New-Lamarckians and the New-Darwinians as the contending parties are called

Weismann as we see, speaks of having declared war against Larmarck's principles; but it is easy enough to see that under the guise of "Neo-Darwinism" he declared war against the foundation of Darwinism.

Weismann denied inheritability of acquired characters and conceived the idea of a special substance to be sought for in the nucleus. "The sought for bearer of heredity is contained in the chromosome material" which contain units each of which determines a definite part of the organism in its appearance and final form"

Weismann asserts that there are two great categories of living material; the hereditary substance, or idioplasm, and the nutrient substance or trophoplasm. He declares that the bearers of heriditary substance "The chromosomes represent a separate world, as it were," a world independent of the body of the organism and its condition of life.

Having thus disposed of the living body as being merely a nutritive soil for the hereditary substance, weismann proclaims that the hereditary substance is immortal and is never generated denovo.

Thus, he asserts "The germ - plasm of a species is never generated denovo—it only grows and multiplies continually handed down from generation to generation. Looked at only from the point of view of propagation the germ cells are the most important element in the individual specimen, for they alone preserve the species, whereas the body is reduced practically to the status of a mere breeding ground for the germ cells which according to Weismann are but the container and nutritive medium of the hereditary substance; they themselves can never produce the latter, they "can never bring forth the germ cells"

Weismann thus endows the mythical hereditary substance with the property of continued exisience; It is a substance which does not itself develop and at the same time determines the development of the mortal body. Further "the hereditary substance of the germ cell prior to the reduction division, potentially contains all the elements of the body" And in the germ plasm there is no determinant of a 'hooked - nose' just as there is no determinant of the wing of butterfly with all its parts and particles. He goes on to emphasize that, nevertheless the germ plasm contains a certain number of determinants which successively determine the development of an entire group of cells in all stages, leading to the formation of nose in such a mode as to result in a hooked-nose exactly in the same way as the wing of a butterfly, with all its little veins, cells, nerves, trachea, glandular cells, form of scales, and pigment deposits comes into being by the successive action of the multitudinous determinants upon the course of the proliferation of the cells"

Hence according to weismann, there can be no new formation of the hereditary substance, it does not develop with the development of the individual, and is not subject to any dependant changes.

An immortal hereditary substance, independent of the qualitative features attending the development of the

living body, directing the mortal body, but not produced by the latter.

The representatives of reactionary biologic science uphold the so called chromosome theory of heredity. Following Weismann the Mendelist - Morganist contend that the chromosomes contain a special "hereditary substance" which resides in the body of the organism as though in a case and is transmitted to succeeding generations irrespective of the qualitative features of the body and its conditions of life. The conclusion drawn from this conception is that new tendencies and characteristics acquired by the organism under the influence of the conditions of its life and development are not transmissible and can have no evolutionary significance.

According to this theory characters acquired by plants and animal organisms cannot be handed down, cannot be inherited.

The Neo - Darwinians hold that the efforts of investigators to regulate the heredity of organisms by suitably changing the conditions of life of these organisms are utterly unscientific. Therefore the Michurian trend in agrobiology is Neo - Lamarckian and unscientific.

Actually it is the other way round. First the well known Lamarckian propositions, which recognize the active role of external conditions in the formation of living body and the inheritance of acquired characters, unlike the metaphysics of Neo - Darwinism are by no-means fallacious. They are quite true and scientific.

Michurians trend is either Neo - Larmarckian or Neo - Darwinian. It is creative Darwinism, rejecting the errors of both and free from defect of Dar-winism

The representatives of Michurian trend contend that inheritance of characters acquired by plants and animals in the process of their development is possible and

necessary. The Michurian teaching as expounded in his works, shows every biologist the way of altering it in a direction required for practical purposes by regulating the condition of life by physiological means.

Conclusion: The recently invented electron microscope has clearly shown the structure of the gene. Now we know that genes are composed of proteins called D. N. A. (Deoxy ribonucleic acid). There are also R. N. A. (Ribonucleic acids) in the cytoplasm and a third substance called the transfer R. N A. which communicate the effect of the gene to the cytoplasm. The experiments done in Russia on a Michurian line of research show that there are graft hybrids which through cytoplasm influence the offspring. But it is not possible to get graft hybrids in all species. We may conclude that both cytoplasm and genes play their role in heredity.

Darwin's theory of Natural Selection

The theory of natural selection was put forth by Charles Darwin. In 1859 Charles Darwin published his essay, "The Origin of species by means of natural selection". Darwin travelled round the world from 1831 to 1836 and during his voyage on the ship 'Beagle' noted down a large number of variations in animals and plants. He also found a large number of intermediate forms connecting two different species. He was also impressed by the fact that plants and animals adapted themselves in a wonderful manner to their environments. Keeping all these facts in view he concluded that the species are not immutable and that new species can arise from old ones by a process of evolution. Darwin based his theory on the following facts.

1. *Rapid Multiplication:* Every living thing in this universe reproduces itself and the rate of increase of the individuals is in a geometric ratio. To illustrate the point Darwin gave the example of the elephant, the slowest breeder amongst the animals. He says that an elephant begins to breed at the age of thirty and goes on doing so until it reaches the age of ninety, producing a young one after every 10 years. It lives up to 100 years. So in all it produces about six off springs if there were no deaths. Darwin calculated that after about 150 years there would be nearly nineteen million elephants alive descended from the first.

Punnet while experimenting on, some Rotifers, which are microscopic organisms, estimated the rate of their increase. They were bred for sixty-seven generations and each individual produced above 30 eggs. The experiment took about a year Mr. Punnet remarks that if he had been able to rear all the animals at this tremendous rate of increase he would have become the possessor of a solid sphere of organic material with the radius greater than that of the earth.

2. *Struggle for Existence*: The prolific rate of increase is common to all living things, animals and plants, living on this earth. But the food supply and space are limited, naturally there ensues a struggle for existence and a large number of individuals born perish before they reach the adult stage. This struggle for existence may be interspecific (between members of different species) or environmental (against the forces of nature).

3. *Variations:* Every individual has its own peculiar character and behaves differently towards the environment. These variations may be of a very small degree, or may be of a greater degree. Then they are called mutations. The individual which happens to possess useful variations will thrive, while the other with adverse variations will perish.

4 *Natural Selection or the Survival of the Fittest*: The individual with useful variation will be best suited to the environment. It will survive at the cost of those brethren which do not exhibit these useful variations and are ill suited to the environment. That is the principle which is called the natural selection or the survival of the fittest.

5. *Structural Modifications*: In order to best suit themselves to the change in environments the individual develops a peculiar character. If this character is passed on from generation to generation it becomes a part and parcel of the progeny. Hence there is a change in the structure or structural modification and a form different from the parents is produced.

Darwin's theory can be tabulated as below :—

1.	Rapid increase in number	Struggle for existence
2.	Food and space limited	
3.	Struggle for existence	Natural selection or the survival of the fittest.
4.	Variations in individual	
5.	Survival of the fittest	origin of new species.
6.	Structural modification	

The theory of natural selection may be summarised thus : There is rapid increase of number in all the living animals, and this over production leads to a keen struggle for existence. No two individuals are alike and every being possesses either a harmful or useful variation. Individuals possessing variations well suited to the environment live and pass on these variations to their progeny where their effect is enhanced. The individuals with less favourable variations either perish or quit the scene of the battle and migrate to places where there is less competition. The enhanced effect of the variation form new species.

Objections to the Theory of Natural Selections.

(1) The theory of Natural Selection takes into account small fluctuating Variations. It is doubtful whether such small Variations confer any advantage on their possessor in the struggle for existence and can be a basis for evolution of new species.

(2) According to the theory useful variations are only perpetuated. The occurrence of vestigial and useless organs is thus difficult to explain.

(3) the transitional forms are not met with.

(4) It does not throw any light on the origin of variations. It explains only the survival but not the arrival of the fittest.

(5) Adaptations due to mimicry are only useful in their perfect state. It is very difficult to imagine that slow and small changes could develop such a perfect state of mimicry and could be useful in the transitional period.

(6) The theory cannot explain the development of neuter flowers and sterility of hybrid.

(7) The power of regeneration in certain animals is attributed to natural selection. Many crustaceans have the power of regenerating their lost parts. It is difficult to explain the possession of such power by natural selection.

Mendalism

Cregor Johann Mendel who is styled as the 'father of genetics' was a monk in Brno, in *Austria* (now a town in Czecho Slovakia). He was a teacher in Brun Realschule and then he became the Abbot of the same monastery. In his spare time he cultivated sweet peas (Pisum) in his garden, cross pollinated them, collected the seeds, sowed them again and carefully recorded the results. He was fortunate in studying single clearcut characters such as height, colour of seed, nature of seed coat etc. After a series of well conducted experiments he came to various conclusion as to the nature of heredity. In 1883 and in 1889 he published these results. But no one appreciated them then. Mendel was much depressed and died soon. But soon in the beginning of the twentieth century these were *rediscovered* and much appreciated. Mendel arranged his results in the form of laws. His theory is known now as ***Mendelism***. Mendolism is the tap root of modern *Genetics*. (The term genetics is derived from the word 'gene.')

His work was done long before chromosomes were discovered and their behaviour studied. We now know that in fertilization the zygote receives chromosomes from both parents. When the sex cells mature in the individual developed from this zygote, chromosomes from the two parents unite in pairs. These chromosomes are known as *homologous chromosomes* because for each unit in one there is a similar unit in the other. These units are known as genes and form the basis of characters of the organism. If the genes for any pair of characters are alike the individual is said to be homozygous for that character. Thus when units for a particular character, for instance tallness, are present in both the chromosomes, the individual is homozygous for tallness. If, however, the genes are unlike the individual is said

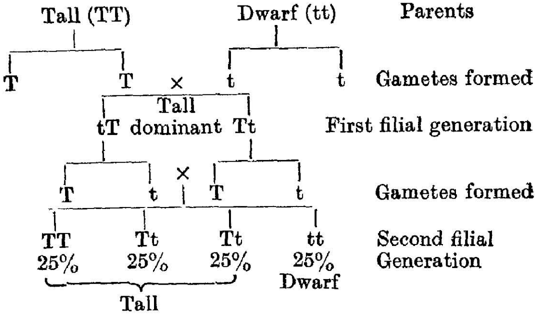
to be **heterozygous.** Thus when the unit in one chromosome represents the character tallness and the corresponding one in the other chromosome dwarfness, the individual is heterozygous or hybrid. The unlike genes of a heterozygous individual are known as **allelomorphs** ; these corresponding characters (tallness and dwarfness) however, do not appear together in an individual, one becomes evident and the other concealed. The one which is shown is called **dominent** and the other **recessive.**

After reduction division when the gametes are formed, each gamete receives only one member of the homologous pairs of chromosomes. The units of the pair, for a character thus become separated (segregated.) In homozygous individuals all the resulting gametes are alike containing the unit for one type of character. The gametes formed by heterozygous individuals are unlike, half the number of gametes containing the unit for one of the allelomorphic characters and the other half containing the unit for the other. Thus individuals heterozygous for tallness will produce 50 % gametes with units for tallness and 50 % with units for dwarfness. If the individuals homozygous for a particular character are bred generation after generation, they will show this one character. If the individuals are hybrid, breeding will betray the fact.

When a homozygous tall pea (TT) is crossed with a homozygous draft pea (tt), the offspring produced in the first filial generation will be *all tall.* Random crossing of the members of this first generation produces in the second filial generation tall and dwarf offspring in the ratio of 3 : 1.

The dwarf pea appears only in the second generation. It was concealed in the first and this character dwarfness is called *recessive* to tallness which is *dominant.* The members of the first generation are

heterozygous containing unlike factors of tallness and dwarfness (Tt). The gametes produced from these contain as a result of the segregation either the tall factor (T) or the dwarf factor (t). The result of random mating of these gametes produces genetically three classes of offspring, such as 25% homozygous for tallness (TT), 50% heterozygous for tallness (Tt) and 25% homozygous for dwarfness (tt). From external features pure and impure tall types, however, cannot be distinguished and the apparent proportion of tall pea to dwarf pea is 3 : 1. This can be illustrated by the following sketch.



4. Mendel emphasized that an organism is made up of a large number of determiners; each of which represents a different unit character which is independent of all other characters.

The results of Mendel's discovery can be summarised as given below.

(a) **The Law of Independent Assortment.** This is the law of unit characters which states that an organism possesses a number of alternative characters or allelomorphs, which are unit characters and are inherited independent of other characters.

(b) **The Law ol Dominance.** When two alternative characters pair with each other, one dominates the other in the hybrid. The character which exhibits itself is known as dominant, while that which remains latent is known as recessive.

(c) **The Law of segregation of characters and the purity of Gametes.** By purity of gametes is meant that the members of the allelomorphs do not blend in the gamete. A gamete possesses only one member of the allelomorphs, *i. e.*, only one of the differentiated characters, either tall or dwarf and not both.

Genetics has evolved considerably after the discovery of chromosomes. Thomas Henry Morgon of U. S. A. won the nobel prize for the wonderful achievements in modern genetics. The study of genetics has now provided a physical basis for mutation or changes in species.

Neo-Lamarckism

Neo-Lamarckism is the theory of evolution supporting Lamarck's view in the light of modern developments put forth by Arthur Canon, Lysenko, and others. The following account is after Canon.

One of the main arguments, infact the main argument of the Mendelians, against 'Lamarkism' was that there was no known mechanism where by an acquired character could be impressed on the germ cell. Why this assumption ever have been accepted? It is obvious that the whole of Mendelian inheritance demonstrated the existance of a mechanism in the reverse direction. According to the Mendelians the germ cells affect the body or soma as it is called—how we do not know. But if the effect can be produced in one direction, why not in the reverse? There is no more mystery in the suggestion that the body should affect the germ cells which is the basis of Lam-

arckism than that the germ cells should control the development of the soma which is the basis of Mendelism. We all accept the latter why not the former? It was maintained that the germ cells were isolated and so protected from outside interference so that changes in the soma would not affect them.

Why the gonads should be considered as more isolated than let as say a muscle. There is no reason why they should not be affected by the whole body- In the same way as some muscle complex or nerve mechanism develops in a particular way during the life of an individual. Then there is no reason why the gonads should not develop in the direction of producing gametes with potentialities of developing into more efficient forms that is forms more perfectly adapted to a changing environment. A muscle system improves with us, why not a gonad ?

Of course the Neo-Mendelians will say that any change in the gametes must occur in the genes of the chromosomes on genes, there is the specific proto-plasm of which of course the chromosomes form merely a part. After all the egg and the spermatozoan of a frog both contain frog protoplasm and not toad protoplasm. It seems atleast responsible to deduce that this may be the reason why together they develop into a frog tadpole and not a toad tadpole !

It has been said any separate mass of one kind of protoplasm will be able to make itself into an individual with the form characteristic of the species. This is regeneration. Many examples are cited. To the *Neo Darwinian of course* it is nothing more than the *gene—complex* exerting its influence on the body. The genes are associated with a particular body form and so, as the process of regeneration goes on, the cells are diverted by a gene complex each into their own alloted place so that the final form of the species is attained.

Now during this century there is an amazing improvement in experimental embryology especially in regards to the newts. This work has been led by the Noble prinze winner Haris Spemann and there in no doubt that it represents some of the most brilliant experimental work ever carried out in biology. Let us describe one of the experiments.

The frog's egg divides into two cells or blastomeres at ordinary temperatures two and three quarter hours after fertilization. If one of the plastomere is killed by a hot needle the remaining plastomere continues to develop as half embryo. The plastomere goes on to develop as if nothing had happened to its partner. However it had been shown long ago that if a frogs' egg that had divided into two cells was forcibly turned upside down an unexpected result would be attained. So a special technique is required to invert the egg. However it is quite simple to carry out and when this is done the egg develops into a double-headed monster. 'Spemann' set out to try to find out what was the control that produced this peculiar result.

He worked on newt's eggs. These are much better than those of frog because the latter has close around the egg proper a layer of shiny jelly which cannot be removed. The newt's eggs on the other hand is naked and can be removed from its jelly 'shell' like pealing peas. The newt's egg in the two celled stage is treated in the same way as the frog's, that is one of the two blastomeres is killed, the other always develops into a complete embryo. The simplest experiment is to tie a knot of hair between the two blastomeres and separate them. They then each develped into a normal but small tadpole. What was the control that determined each half should develop not into a half embryo but a whole one ?

This experiment can be carried out much later than the two-cell stage at the stage when the embryo is a hollow sphere of cells what we call the blastula.

But an even more illuminating result can be obtained at this stage if two blastula are each cut into two each one on the leftside and other on the right side. This produces two small and two large pieces. These pairs then can be placed together, small with small and large with large, when they join up and heal as composite organisms, one smaller than normal and the other larger; but in both cases absolutely normal in their propotions.

This last fact illustrates another point, when the vertebrate eye is formed, it starts as a hollow outgrowth of the front division of the brain. As this pushes its way towards the skin at the side of the head it becomes cup shaped, the opening of the cup facing outwords. The skin overlying the cup thus stimulated and develops as a thinkened patch into the lens of the eye. Now in the larger of our two composite newt's embryos the outgrowth is larger than normal, in the other it is smaller. But in both the cases the lens produced is of the right proportion. Can this be due a Mendelian mechanism? Is it not more likely that the organism acting as a whole is controlling the relative size of the different parts by some mechanism other than the gene complex?

There is a further type of experiment which demonstrates this even more clearly, those experiments where patches of cells of bastulae of Amphibia, that it is of the whole group containing the newts, frogs and toads are grafted into strange position in embryos of different species or even different genera. Do not think that these grafting and transplantation experiments are particularly difficult. Of course a certain amount of technical skill is required and fine pipettes and scalpels are necessary but the most important factor is the amazing power of recovery of the embryo. The grafts heal into positions in hours rather than days.

There must be a dual control of the development of any organism, but more than this, it shows how the

organism itself can control the individual cells of its body. If a body can force strange cells which have been experimentally introduced into it to develop functionally according to its will. Why then if an organism develop new characters in association with new environment—why should it not be able to force its own germ cells to reproduce those new characters. This is what the anti 'Lamarckians' deny.

However let us explain a futher case. In normal development the lens of the amphibian eye develops as a result of a stimulus from the eye cup which grows out towards overlying skin. Now it happens that if the lens of the eye of a newt is, removed, the animal has the power of regenerating the lens. There is nothing strange in that but what is strange is that it regenerates it not by the normal process of development at all but by something quite different, by a special out growth from the upper side of the iris. Now this ability is a character which more over distinguishes newts from frogs and therefore it must be represented according to the Neo-Mendelians somewhere by genes in their own particular places on appropriate chromosomes. But even more fantastic than this, according to the New-Darwinians it must have been established by means of Natural Selection. This I suppose is what was meant when it was said that given time anything at all will turn up for. For how often has Natural Selection had the chance of acting in such a case? How often does a newt have the lens its eye accidentally extracted so that Natural Selection can pick out for survival the fortunate newt that is able to regenerate its lens by an amazingly lucky chance of having developed a specially new process just for the occasion?

Whatever that may be which knows and with what it wants to produce it is the harmonious control that Waddington had to call into help

himself out of his dilemma when he broadcast to the world the 'orthodox' theory of evolution! But more particulary it is the power behind true Lamarckism, the power which Lamarck of necessity postulates in his second law. It is the organism itself by its relation to it environment that is by mere living that calls for new organ or new habits. These do not arise by mere chance as Darwin and the Neo Darwinians would have us to believe. The urge comes from inside the organism. It is as Samuel Butler so aptly called as the internal design. Taking example of cases from comparative anatomy. Lamarck's hypothesis implies that it is the needs of an organism that determine the course of its evolution to evoluate it we must be sure that we know what those needs will be and this often leads on to dangerous ground. We take simple physical principle. Firstly in the blood system of all vertebrates valves always occur at appropriate places, along the course of the blood vessels and are so constructed and orientated as to ensure the passage of blood in one derection. It may be argued that since there is a heart and that heart is a pumb this would be certain for a pumb must contain a valve. On the whole this is correct but it would be a very inefficient system by itself. The difficulty which has to be overcome is that when a muscle contracts it fastens and naturally presses on any adjacent blood vessel this squeases the blood in the vessels and tends to force the blood out of the vessel in either direction. If this was allowed to happen muscular activity would impede the steady progress of the blood from the body and more over the greater the activity the greater the hindrance. To overcome this, valves appear along the blood vessel so that when a blood vessel is squered the blood tends to force out of it but in one direction only. Therefore muscular action is only an accessary factor for circulation.

Birds evolved from reptiles by developing the power of flight. Therefore reduction of weight be-

comes necessary for flight. In birds this necessity has been brought out in a most ingenious manner, air sacs have developed as outgrowths of lungs and extend into various parts of the body. They even enter the bones. The bones of a bird are hollow. Thus without diminishing any way the strength of its skeleton by filling its long bones with air the bird has become lighter. A new method of excretion which involve the use of little water was necessary in birds to reduce weight and so it evolved. Excreta in birds is in a crystalline form.

When the bony fish first appeared they breathed by means of gills. Due to the defficiency of oxygen in water as in the tropical swamp in these fishes evolved an outgrowth of the hinder part of the throat as a bladder in which bubbles of air could be stored and at the same time develop the ability to use the gaseous exygen. For respiration along with the dissolved oxygen that attained through their gills. Bony Fishes which have evolved air bladder use them to control their own density They gave up using it as a lung and relied once again on their gills and then by secreting oxygen from their blood into the air bladder they could enlarge it and make themselves more buoyant. Whereas by extracting air from the air bladder into the blood they could diminish their air bladder and make themselves more dense. Therefore they could extend to the greatest depths of the ocean.

Filter feeding mechanism occurring in ininvertebrates and in the larvae of Lamprey are adaptations by which an animal can live on small food particles much too small for its fellow creatures without such a filter. In crusacea such a mechanism always consists of inter related limbs or parts of limbs arranged in a special relationship to the mouth. There must be a filter and some form of apparatus to draw water through the filter. Then the scraper must be present to remove the residue from the filter plate and finally

there must be a transport system to convey these materials to mouth as food. Such an apparatus in crustacea has evolved atleast along six different lines. It would seem without doubt that in each case a necessity arose through a competition for food of feeding on minute material. The need was there and the apparatus evolved.

The difficulty of amphibia to evolve into reptilia had to be overcome by the fact that the amphibian laid its eggs in water while the reptile had to lay its eggs on dry land. This involved the provision of an egg shell to prevent the albumen from drying up. In the reptilian eggs if the waste products were to diffuse out into the albumen they would prevent up its giving up water to the developing embryo so a new structure developed. This is simply an early appearance of a cloacal bladder of the amphibian. It appears as an out-growth of the hind gut and is called the allantois. It is a most important organ for it becomes later in evolution the placenta in mammals The egg was to be laid on dry land and so must be hard. The embryo had to get out of the shell and so had to be provided with a special opener and incidentally the knowledge of how to use it. This has appeared in a variety of ways as modified tooth in some snake and lizards while later in birds it is a nodule near the tip of the beak.

There are other major changes in the adult forms in connection with reproduction and respiration. All these changess are interdependent. The albumen could not have arisen without the shell and allantois. The shell would not have appeared with out the egg opener. Any one with out the other would he senseless, they must have evolved together. And this is according to Darwin and Neo-Darwinians, we are asked to believe is the result of random variation.

The valves in the blood vessels throughout the animal kingdom, the parts of the filter feeding mecha-

nism the adaptation to flight, all, are obvious solution to environmental troubles. None of them can be accounted for by the inherited effects of use. However much blood passes down a blood vessel it cannot directly cause a valve to appear. However much a bird flies it cannot force air into its bones. However many eggs a lizard may lay ' the act can not cause the embryo to develop its most ingenious built an egg — opener. Then Neo-Mendelians attribute all these amazing adaptations merely to a fantastic succession of lucky hits. Lamarck says that they arose from a power within the organism which ensures that any need which the organism experience in the changing environment is met by the production of the appropriate adaptation. The famous giraffe neck illuminates the difference between Darwin's and Lamarck's points of view. But Lamarck's views have been without exception entirely misrepresented. It was Wallace who made the first mis-statement. He said that according to Lamarck the giraffe acquired its long neck by desiring to browse on the higher trees and from that day to this it has been the evolution of the neck of the giraffe which had been held up to redicule.

What actually Lamarck said, that the animals continually strove themselves to reach higher leaves on the trees and it is reasonable to interpret this to mean that the animals developed the habit of continually reaching upwards by pushing themselves upon their front legs and as a result this became elongated. It cannot be denied that the continued extra pressure put on the ends of the long bones of the front legs might stimulate those bones to elongate. But now apply the same to the neck. It has been said by all authorities that according to Lamarck the animals strove to elongate its neck and so it elongated. But the fallacy is that neither giraffe nor any other vertebrate can strive to stretch its neck. A neck can be stretched out but it cannot be stretched! The act of

stretching *out* a neck might in fact by pressure on the intervertebral element slightly diminishes the total length of the neck but it cannot increase it. It is morphologically impossible. What he actually said was that the front legs elongated in the way described and the neck elongated accordingly. There was a need of a long neck to correspond to the long leg. There being the need then according to Lamarck's second law that need was satisfied.

A similar case ofcourse occurs in elephant. The modern elephant develops its massive head to smash down trees and eat leaves. So the neck became short and stout. And to reach water at its feet it has to elongate its *snout. To return to the case of giraffe* what Lamarck said was logical. The real story of evolution of the giraffe is probably quite different from either view. The trouble is that the female giraffe is 2 or 3 feet shorter than the male and so if natural selection has anything to do with it only the males would be selected for survival and that would be disastrous. The long neck is probably incidental.

It is more likely that the long legs developed as a powerful means of running at speed. Now the natural enemies of giraffe are lions and this ability of running very fast must serve them in good stead in escaping. But the *important part of an escape is in the first split* second. The animal may be able to get a move on immediately it senses danger. That the reason why the giraffe retained relatively short hind legs. By means of these the body can be put in motion much more quickly than if they were the same length as the front legs in the same way as a car moves off in low gear and only changes into top when already moving. The giraffe does the same. It makes the quick get away with the low gear hind legs and changes to the top gear of its front legs.

Neo-Mendelism

The Particulate Theory of Inheritance.

The Particulate theory of inheritance is due to the genius of Gregor Mendel, the abbot of Brunn. He communicated the results of his work on heredity to Brunn Natural History Society in 1865, and they were published in its '*Transactions*' the following year. Mendel left his conclusions in the form of two very *simple laws.* First that when purebred individuals are exhibiting a pair of contrasted character, are crossed, the original types separate out in definite proportions in the *second filial generation,* that is among the grand-children. This process is is called *segregation.* It makes no difference what may happen *in the first generation* of the cross. This is made up of hybrid individuals, one of the two characters may be obscured by the other or some condition intermediate between them may be found. The essential is that no blending has occurred, as is proved by the recovery of the grand parental types in half of the next generation, the reminder being again of the hybrid constitution.

Secondly Mendel asserted that when two or more pairs of contrasted characters are brought into the cross they *Segregate* independently of each other. This principle known as the law of independent assortment has, however, been modified by subsequent discoveries (as explained in Linkage).

In Mendel's day the phenomenon of segregation, and the constant numerical ratios in which the different types crystallize out of the hybrid mixture, could not be correlated with any known mechanism. But in the thirty five years which elapsed before results attracted general attention, great advances has been made in cytology. It had become apparent that the hereditary material must be carried in the nucleus of

the germ cells for this is often the only part which the offspring receives from both its parents. And in the nucleus had been found self perpetuating bodies, the chromosomes which exist in pairs whose members having separated from each other are recombined at fertilization in a manner well fitted to provide the physical basis of the Mendelian segregation of characters.

This close parallel between the genetic requirements and the facts of cytology was first pointed out by Sutton (1902). Modern work especially that of the Morgan School has built up a vast body of facts which make the evidence for the chromosome basis of heridity, remarkably complete. It may therefore be of value to give a short account of Mendel's two laws in the light of these discoveries.

A. Segregation. Inherited characters are dependent on the action of certain genetic factors or 'genes' which control them. These are present in pairs, whose members are derived one from the father and the other from the mother of each bisexually produced individual. The paired genes are carried in paired bodies, the chromosomes of which every somatic cell in the organism has a complete set in its nucleus. The mature germ cells however contain one member of each chromosome pair, consequent upon a process called meiosis in which, they conjugate, separate and pass at random to opposite poles during cell division. The total number of chromosomes and therefore of genes, is restored when the gametes, each carrying half, fuse at fertilization.

The members of each factor-pair are called 'allelomorphs' and from what has already been said it is evident that they are carried in different but homologous chromosomes at rare intervals. The physical or chemical nature of a gene may change. This Process called gene mutation is ultimately responsible for the

fact that the members of allelomorphic pairs may exist in two or more conditions. A number of such changes may occur in the same gene and so form a series of 'multiple allelomorphs', only two of the members of such a series can of course normally be present at the same time.

If the members of the allelomorphic pair are of similar nature they are said to be 'homozygous, if dissimilar heterozygous. In the latter event their effect may be intermediate between that which either produces the pure, or homozygous condition or more generally the presence of one type may obscure the action of the other. The former is then known as the dominant and the latter as the recessive character.

It is evident however, that whatever the heterozygous effect may be, no blending has occurred, for owing to meiosis during maturation, the unlike members of the factor pair segregate from each other in the separating chromosomes to produce germ cells, carrying either one or other type, thus giving rise to fresh combinations in the next generations.

B. Independent Assortment.

In the second law Mendel stated that two contrasted characters behave independently of each other when inherited together. From what has so far been said of the mechanism of heridity the truth of this statement must be obvious so long as the factor-pairs in question are situated in different pairs of chromosomes. In such circumstances their allelomorphs will segregate form each other during meiosis and pass in to germ cells at random.

It is evident that when individuals with two contrasted pairs of characters, each exhibiting complete dominance are crossed, four types will be produced in the F2 generation. These represent the original distri-

bution of characters and the two possible recombinations between them. Since each type considered separately will appear in a 3 : 1 ratio in this generation the four will together be present in a combination of 2 such ratios ; that is to say in the ratio of 9 : 3 : 3 : 1. This is called dihybrid ratio.

C. Linkage

The number of genetic factors in any individual must be very great amounting atleast to several thousand. It is rare to find a species having more than three or four dozen chromosomes and often there are much fewer. In 'Drosophila melanogaster' in which so many genetic problems have been studied there are four. It is evident therefore that each chromosome must contain many factors. These will be inherited together for at meiosis, they will pass in to the same germ cell with out the opportunity of random assortment. This is known as linkage.

If a back cross is made between two linked factors it is therefore to be represented in F 2 generation. The recombination classes will be absent for free assortment only occurs when the pairs of factors or in different pairs of chromosomes.

It is important to notice that in linkage no association exists between the factors as such except that they happen to be carried in the same vehicle. Thus two linked homozygous dominants may be brought in a cross by one parent and their recessive allelomorphs by the other. Then when the F 1 generation is back crossed, the two grand-parental types will appear in F 2 in this instance the double dominants and the double recessives. If however each parent brings in the dominant allelomorphs of one pair and the recessives of the other, on back crossing to the double heterozygote it is again the grand-parental types which appear; the double dominant and double recessive classes are now absent. The factors which go

in to the cross together come out together whichever way they may happen to be assorted.

Linkage of course holds good for all the factors situated in the same pair of chromosomes however many there may be. Such factors therefore are associated together in a 'linkage group'. On the chromo some theory of heridity there can be no more linkage groups in a particular species than there are pairs of of cromosomes.

D. Sex Linkage

Sex is inherited as a pair of contrasted characters segregating in a definite proportion which is generally near equality. It therefore partakes of the nature of particulate inheritance and is infact dependent upon the action of one or more genes carried in a particular pair of chromosomes called X-chromosomes. The remaining chromosomes not directly concerned with the determination of sex are together known as the autosomes.

In one sex there is a pair of X-chromosomes, just as there is a pair of each of the autosomes. In the other sex there is but a single X-chromosome whose partner is almost destitute of genetic factors and is in general not concerned with sex determination. This is the Y-chromosome. The former having similar sex-chromosome is known as the homogametic and the latter as the heterogametic sex. It is a highly remarkable fact that the heterogametic sex in some forms the male and in others lepidoptera, the birds, some fishes and amphibia, it is the female.

From what has already been said on the subject of linkage it is to be expected that the X-chromosomes will contain many factors other than those for sex, with which however, they will necessarly be linked. Thus sex linked factors then are inherited relative to sex unlike those situated in the autosomes.

E. Crossing-over

Linkage, however, is not always complete for an exchange of substance and therefore of genes, may occur between the chromatids derived from homologous chromosomes during the prophase of the first meiotic division. This is known as "crossing-over." At this time the chromosomes become spun out into thin threads which twist round each other. Subsequently each splits longitudinally, forming a pair of chromatids. In drosophila, for example certain genes prevent a breakage occurring in their immediate neighbourhood while no crossing over is possible in the males of this genus; indeed in all forms it appears to be less frequent in the heterogametic than in the homogametic sex. On the other hand the frequency with which a breakage and interchange may occur between any two factors is constant in the same conditions. It is important very briefly to study crossing-over and the light which it throws on the mechanism of heredity.

If two individuals, one homogygous for the dominant and the other for the recessive allelomorphs of two pairs of factors are mated, double heterozygous offsprings are produced. It had been pointed out that when these are back crossed, then if the two pairs of factors are in different pairs of chromosomes, free assortment takes place. The two grand parental types and the two possible recombinations between them all appear in equal numbers.

If however, the factors are in the same pair of chromosomes, and complete linkage exists, the two grand parental type only will segregate out. But when crossing-over occurs there appear in addition some individuals belonging to the recombination or cross-over, classes. In order to estimate the amount of crossing over these are added together and expressed as a percentage of the whole. This is known as "cross-over value."

When the cross-over values of the three factors situated in the same chromosome are studied, it is found that an important relationship exists between them. For the cross-over value between the factors A & B added to that between B and C is equal to the cross over value between A and C. The closer together any two factors happen to be the small is the chance that crossing will takes place between them. Thus we arrive at a definition of allelomorphism, " allelomorphic factors are situated at identical loci in homologus chromosomes".

F. Mutation

Many meanings have been applied to the term mutation. It is convenient to restrict it to the inception of a heritable variation. This may take the form either of a gene mutation which is a change in the genetic factor or a chromosme abnormality.

Gene mutations are responsible for the fact that the allelomorphic factors may exist in two or more conditions. They are consequently of fundamental importance of heredity and evolution. They are of very rare occurrence, so much so that it is most difficult to estimate their frequency. Even in Drosophila melanogaster, of which far greater numbers have been studied than of any other animal, such an estimate is rather untrustworthy, for the number detected will greatly dedend upon, the skill of the observer. It would seem that a given gene seldom mutates in more than one individual in three hundred thousand, usually more rarely. Mutation at one point in a chromosome is not accompanied by simultaneous mutation at other loci. It can occur in the body cells as well as in the germ tract, so giving rise to 'somatic mutation'. This results in a mosaic appearance similar to that some times produced in heterozygotes by the dropping out of a chromosome, due to a failure in mitosis. When this occurs in homozygote it must be attributed to somatic mutation.

Gene mutations can be induced by short wave radiation from X-rays and their frequency may be increased atleast fifteen or twenty thousand percent by this means. The rate of increase appears to be proportional to the energy of the dosage absorbed and is independent of the wave-length. The greater frequency of gene mutations at the white eye locus of the Drosophila melanogaster as compared with other loci where only a single change has been detected is certainly statistically significant. On the whole it seems that those loci which mutate most frequently in normal condition produce the most mutations when treated with X-rays.

It is possible to suppose therefore that the artificial induction of mutation is concerned in raising the general level of the mutation rate.

The type of change which occurs at gene mutation has been a subject of much controversy. In the past many workers have been led to the conclusion that a physical-loss of material takes place. That gene mutations however must often represent chemical changes rather than physical losses is indicated by the proved fact of reverse mutation. It is hard to conceive of mutations occurring in both directions with a frequency at all comparable to each other if an actual loss were involved in the original change. It has, however been pointed out that some gene mutations may in fact represent physical exceptional and the evidence for their occurrece is quite other than that which led to generalizations on this subject in the past.

The occurrence of chromosome abnormalities may also lead to hereditory changes. These are to be divided into two distinct classes — exceptional fragmentation of the chromosomes themselves and abnormalities in the distribution of whole chromosomes.

The first of these types occurs naturally, though very rarely. It is however, quite a frequent result of

treatment with X-rays. Portions of chromosomes may break away and become attached either to the homologous chromosome or to one of the other chromosomes, while sections of a chromosome may be lost, so giving rise to deletion.

The effect of heteroploidy is generally deleterious since the genic balance is upset. but a balance multiplication of the chromosome number is free from this defect. The forms in which this has occurred are known as autopolyploids. These are usually fertile with one another but not with individuals whose chromosome number is a different multiple from their own. Thus they are capable of originating a new stock which may evolve along its own-lines and lead to a specific difference.

The chromosome of a polyploid may be derived from two different species. Hybrids between different species should contain the haploid number of each. They are generally sterile since the chromosomes have no identical partners with which to conjucate during meiosis. If however they double this number producing an allotetraploid, each chromosome gains a partner and fertility is restored. In this way fertile hybrids sterile with both their parental forms may be produced. This is a near approach to the formation of a new species. It has occurred under experimental conditions and it has done so in nature.

Polyploidy then has played a part in the evolution at least of plants. But the changes it initiates are often considerable and then they must be very unimportant in animals, for they are rarely self-fertile and turthermore their mobility and quantitative sex determining mechanism will lead to prevent the establishment of this type of mutation.

Summary

Mendelism is a particulate theory of inheritance. Characters are due to the action of pairs of factors and

these are carried in paired bodies, the chromosomes, whose members are derived respectively from the two parents ; they separate from each other again in the germ-cells.

The factors may exist in two or more conditions so producing contrasted characters. When two individuals with such chracters are crossed the original types segarate out, or segregate in definite proportions in subsequent generations.

The number of chromosomes is constant in a given species and each contains many factors The pairs of factors segregate independently of each other, if situated in different pairs of chromosomes, if in the same pair, they are 'linked' and inherited together. Sex is dependent upon genetic factors carried in a pariticular pair of chromosomes. They have a quantitative action. Numerous other factors are carried in the sex chromosomes and hence are linked with sex. In many instances an orderly interchange of material takes place between pairs of chromatids derived from homologous chromosomes. This allows the recombination even of linked factors which 'cross over' with the substance exchanged from one chromatid to the other. The factors are arranged in linear order on the chromosomes and are situated at definite loci.

Mutation the inception of a heritable variation, may be due to changes in individual factors, or to fragmentation of the chromosomes on irregularities in their distribution. It is a phenomenon of great variety, but it can be inducod artificially. Almost all heritable variation owes its origin to such mutation.

What is The Origin of Species?

WADDINGTON

Although the book that sold the theory of evolution to the scientific world was called, "The Origin of Species" it is precisely the problem of how species originate that remains one of the most mysterious questions in the whole complicated edifice of theory and fact that has been built up in the hundred years since Darwin wrote. We have made great advances in understanding how the character of a group of animals or plants may gradually change as the generations pass. This is the progressive aspect of evolution. Species differences are not quite comparable to those we find existing contemporaneously in the world of today. In the origin of a later species from an earlier ancestral one there need never be a stage at which the population of animals is split into two separate groups; the later species may be formed merely by a gradual progressive alteration of the whole population. On the other hand, the many different, but related species that exist simultaneously at a single time must if they are produced by evolution have been formed by a process that involved splitting up an originally single population into a number of distinct sub-groups.

Since Darwin's day we have discovered a great deal about the nature of the differences that exist between such contemporaneous and related, but yet definitely distinct, species. We know that in many cases the species difference may involve changes in the arrangment of the chromosomes which may have been broaken and rejoined in various ways. Such chromosomal alterations can be detected by cytological study in particular of hybrids between the two species, of those can be produced. The evidence suggests however that such comparatively crude changes as a reshuffling of the chromosomes are not an essential feature of species divergence. They seem more usually to be secondary effects which have occurred after the initial stages an the splitting of in originally single species in to two sub-units.

A much more important fact is that each species has a characteristic integrated system of heredity and that these systems differ from one species to the next. As Th. Dobzhansky in particular has emphasized this common 'gene—pool' is not just a haphazard assemblage of individual genes; on the contrary it is integrated in the sense that genes belonging to one gene-pool fit in reasonable well with the other members of the pool. On the other hand genes belonging to one species may not fit in at all well with the gene pool of some nearly related species; the hybrids will be unhealthy, or infertile, or ill-balanced in some other way.

This organisation of the heridity endowement of a species is spoken of as the 'Co—adaptation' of the gene-pool. Co—adaptation occurs not only with in the species as a whole but to a minor extent atleast with in separate populations belonging to the same species. Differences in Co—adaptation tend to occur whenever two populations fail to interbreed. The barrier between them may be merely distance, so that the members of one population, although they would be ready to breed with the members of a second population and would be perfectly fertile with them, never, in fact come across them. It two populations, belonging to the same species remain for a considerable time with little interbreeding it is found that their co—adapted gene pools have diverged to some extent. It seems that the most typical cause for the differences in co-adaptation bet ween different species is their failure to inter-breed.

But the lack of cross-breeding must be continued for a long time if two populations are to diverge sufficiently to be ranked as different species. The co-adaptation of the gene-pool of a particular group must arise only very gradually, as natural selection weeds out those genes which although not specially harmful in other combinations happen not to fit on well with the constellation of genes that is becoming characteristic in this population.

That brings us back to the other difference which, we know, very frequently exhibits some other barrier to cross-breeding that is not dependent on distance. This very commonly takes the form of a disinclination of the individuals of one species to mate with those of another. The existence of a reproductive barrier of this kind between species is not universal. Clearly when it is in existence it will make it much easier for the gene-pools of the two groups to diverge, since it will prevent the mixing that would tend to bring them back to uniformity.

One of the Great puzzles in understanding the origin of species is to discover how these reproductive barriers arise if one has a uniform population of animals, all of which are perfectly ready to mate with any member of the opposite sex. We therefore have to think of some special methods by which the first steps in sexual isolation could occur. From a theoretical point two suggestions have been put forward. One is often associated with the name H. J. Muller, who attributes the origin of Sexual isolation to pure chance. This amounts to saying that we just have to accept it as an empirical fact that, when the gene-pools of two groups start to become differentiated from each other, one of the first signs will be that the populations begin to acquire different sexual preferences, which will cause individuals to tend to mate with in their own population rather than crossing with members of the other. The alternative suggestion is to point out that as soon as the gene-pools of two groups have diverged somewhat the hybrids between the populations will-end to be inferior and that there will be a natural selection against the readiness for cross breeding. The point has been particularly emphasized by Dobzhansky, who has suggested that this type of selection against readiness to cross-breed may be involved even in the very first stages in the evolution of a reproductive barrier.

So far little experimental work has been done on this problem. It is obviously very difficult to investigate in nature the situation of species as they begin to become

distinct from one another. One can discover populations which seem to be in the first stages of species divergence and one can show that they may differ in such matters as mating preference, but it is almost impossible in such cases to discover how these differences in reproductive behaviour have originated. Many experiments have been done with Drosophila melanogaster and we are much satisfied with the results.

Geographic Subspecies and Neo-Darwinian Evolution :

DODSON

An important aspect of natural species is the fact the various types of variablity occurring with in a species are not scattered evenly over its entire range, but rather that local populations commonly more or less isolated from their neighbours, show distinctive patterns of the variable characters of their species, with the result that they may be defined as sub-species. They are fertile in crosses, and intergrades between adjacent sub-species are commonly found wherever their ranges meet. But the several subspecies of any one species do inhabit ranges which are mutually exclusive for the most part. Closely related species may have identical ranges, but sub species replace one anothers' geographically. The whole series of geographic sub species for any species is called a Rassenkreis.

Wherever sub species are distributed over an area which presents a progressive change in some physical feature, such as mean annual temperature some of the differences in the sub species are likely to show a progressive change also. Such series are called 'clines'. One can scarcely doubt that such characters which vary progressively along with or progressive change in climate or topography, must be of adaptive value to the various subspecies concerned. In Primula (primrose) there are "ecotypes" adapted to alpine habitats and there are

ecotypes adapted to meadow lands. Here again one can doubt the adaptational value of a character complex which is always found in plants, which live in particular type of environment. Wherever such ecotypes form a cline they coincide with the sub species. Sometimes factors leading to such cline formation can be summarised in concise rules. Thus Bergmann's rule states that in a given species or genus, northern population have a larger mean body size than do southern populations. This is believed to depend upon the fact that a large body has a smaller surface area per unit volume than does a small body. A corollary to this, Allen's rule, which states that extremities tend to be smaller in the north than the south. Again this is interpreted in terms of restriction (north) or extension (south) of radiating surfaces. Arctic animals have very effective insulation of fur or feathers as well as circulatory control of heat loss. The less protected extremities are physiologically adapted to function well even when thoroughly chilled. Probably the physiological adaptations are of major importance, yet under conditions of severe competition even the small additional advantage gained by size variation in accordance with these rules is sufficient to give a selective advantage to those populations which conform. Exceptions to these rules can be found but they have considerable validity.

Sub species need not occur in clines. That is, if a series of sub species A, B, C, D and E occur in that order over the geographic range of the species, A might resemble B in size while it resemble D, most closely in color. In a third character it might resemble C most closely and so on. Sub species of North Sea-herring, for example have been defined by means of statistical studies of such characters as number of vertebrae, number of scales in the lateral line, number of rows of scales above and below the lateral line and many other variable characters. The resulting statistics show that the averages and standard deviations for each school are typical and

differ from all others, with the result that they may be described as sub-species.

Now Darwin had already spoken of sub species as "incipient species... ... which .. ...become ultimately converted into good and distinct species.... . by... ...natural... ...selection." As already mentioned Darwin realised that the weakest point in his theory was the lack of knowledge of heredity. The dominant school of evolutionary thinking today is based upon the Darwinian principles of the prodigallity of nature, variation and natural selection. But to this is added the interpretation of variation in terms of the theory of the gene and the study of population and changes in gene frequency with the tools of statistics which like genetics did not exist in Darwin's time. This school is therefore known as the *Neo-Darwinian School*. This is exemplified by most of the outstanding students of evolution of today, as Sewall Wright, Th. Dobzhansky, G. L. Stebbins and Julian Huxley.

For the Neo-Darwinians, then, sub-species are, at least potentially, incipient species. Each sub-species of a particular species is characterised by a particular complex of gene-determined characters and these various genes are derived by mutation from an originally more uniform progenitor. The genes which any particular sub-species have are not peculiar to it. It is the constellation of genes which is unique for each sub-species, not the individual genes. Such gene combinations are the materials upon which selection acts. With in such sub-species mutation continues at random with the result that different alleles arise in different sub-species. Now sub-species are usually at least partially isolated from each other geographically.

Other types of isolation may also arise for example physiological or ecological isolation. Thus by the gradual accumulations of mutations such isolated sub-species may "become ultimately good and distinct species."

The spectrum of mutation extends from gross defects such as lethality or crippling through moderate effects like color change or change in bodily proportions. Neo-Darwinians generally fovour these minor changes, for several reasons: first, most of the larger mutations are plainly abnormalities which would be eliminated by natural selection. This may be a consequence of the fact that the more favourable one, which must have recurred many times in the past because of the high natural mutation rate, have already been incorporated into the normal genotype of the species. Secondly, it is generally accepted that a species can harmoniously incorporate in to its genotype a series of small mutations more readily than it can a single, equivalent larger mutation. Most important is the fact that sub-species and closely related species generally differ from each other in a series of quantitative traits, such as size, proportion, color, or extent of a pigmented area. As explained above such traits are generally inheirted upon the basis of swarms of genes each with a very small effect individually.

This theory is plausible in every detail. It has the advantage of incorporating the greater part of historical Darwinism with some of the main trends of modern genetic research. It is backed up by a great body of experimental data. It is hardly to be wondered at then that this theory has achieved very nearly universal acceptance.

Difficulties of Neo–Darwinism. Goldschmidt believed that the Neo-Darwinian type of evolution by accumulation of micromutations under the influence of natural selection, is largely restricted to sub-specific differenciation with in species and that the decisive step in the formation of new species must involve an altogether different genetic process, the systemic mutation. If Neo-Darwinian evolution gives rise to new species then new species should come only from the terminal members of a Rassenkreies. He beleived that good species are

always separated from their nearest relatives by a bridgeless gap. Controversial cases be beleived depend in part upon purely morphological definitions of species which do not take the genetic facts into account. Goldschmidt believed that interbreeding, or pottentially interbreeding population should be treated as a single genetic unit, a species from an evolutionary point of view even if other factors may take it advisable for taxonomists to break it up into several species. On this basis many difficult cases can be resolved in accordance with his ideas.

Another major Neo-Darwinian tenet is that isolation of a sub-species is essential if it is to accumulate enough gene differences to become a good species, distinct from the parent species. There is a race of Lymantria dispar (gypsy moth) which has been isolated on the island of Hokkaido (North Japan) since the early tertiary period, yet in the intervening 60,000,000 years only sub-species deffenciation has occurred. Again the seasonal variation with in a single race of papilio (butter fly) may be greater than the variation between races at any one time.

Finally, Goldschmidt believed that the Neo-Darwinian theory places and so great a burden upon natural selection. The theory demands that only very minor mutants be significant for evolution and there would be subject to very slight selection pressures One may define selection pressure in terms of loss of survival value. Thus if 1000 individuals of genotype A A survive to reproductive age while only 999 of genotype a a survive, the selection pressure against a is said to be 0. 001. If the favored gene is dominent, it would require 11 739 generations to raise the frequency to two in a million. But if the favoured gene is recessive, 321,444 generations would be required[1] Selection operates more rapidly when the gene frequencies are higher.

There is no doubt that the majority of geneticists, as well as other students of evolution, do not agree with

Goldschmidt with respect to some or all of his thesis. But most will agree that he has amassed a body of highly pertinent evidence which can not be lightly dismissed.

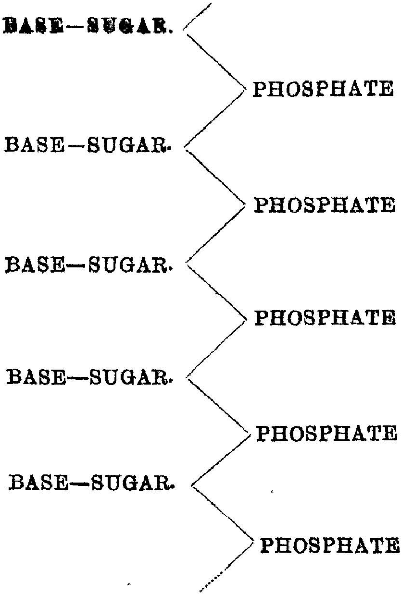
Perhaps these views are not so divergent as they seemed only a few years ago. At the centre is the theory of gene. The implication of physiology for morphology and the morphology for physiology were not clear. Certain recent developments have tended to clarify it. First the great development of biochemical genetics in recent years has focussed the attention of geneticists upon physiological aspects of gene. Second, increased interest in pseudo-alleles has tended to blur the limits of the gene and to leave the corpuscular theory as merely as a first approximation. Finally much recent evidence points to desoxyribonucleic acid (D. N. A.) as the actual genic material. Nucleic acids are made of nucleotides each of which consists of a pentose (five carbon sugar), phos phoric acid, a base, which may be a purine [adenine (A), or guanine (G)] or a pyrimidine [cytosine (C) or thymine (T)]. These are polymerised by sugar phosphate linkages to form long chains, on which the bases appear as side chains.

X—ray diffraction studies showed that there are always two such chains spiralling about a coman axis. They concluded that the bonds of D N A chains are either adenine and thymine or by cystosine and guanine.

One current theory of the gene sees it as a more or less broad field of function with a point of focus on the chromosome comparable to the centre of gravity of a physical object. The data of the corpuscular gene theory such as crossing over deal with these point foci. While position effects and pseudo-alleles deal with the broader fields. These functional fields may vary in size from molecular dimensions to the entire separate as required by cross over data. This Theory embraces elements of both the divergent views of a few years ago, and it may

well sub-serve species formation upon lines related to both theories and perhaps according to others still unformulated.

D. N. A.



The Structure of D N A shown by Watson and Crick. The sketch shows the pattern of polymerization!

Effects of Geographic Isolation

Barriers of different kind combine to produce an isolated area. Climatic barriers, also exist which usually show a less definite boundary than do physiographic barrier's. As we know barriers have two fold effects. 1. They separate closely related forms and thus they prevent interbreeding 2. They make possible independent differenciation of two groups. Barriers protect the species with in their isolated range from the competition of rival animals.

Isolated animals develop in different directions in a short time, as Cattle in the island of Jersey. Wagner was the first to emphasise from the evidence of distribution that geographic isolation must have an important effect upon the transformation of species and the formation of varieties and sub-species. He even believed that this is the only way by which one species can become differenciated from another, failing to take in to account other means of interbreeding prevention. The most important other means is the physiological isolation. Isolation furthers development of new races based on the non-adaptive charaeters. Isolation if removed from a gronp of enemies may also make possible the development of structures or colours which would otherwise be eliminated

The varying effectiveness of barrier in separating interbreeding communities is of great importance to mutational evolution With complete isolation the group, first differenciates into varieties and sub-species and then with longer periods of time vary into wholly distinct genera and even families.

The isolated form is *endemic.* The longer the isolation continues the larger is the number of mutation that occurs and greater is the divergence from forms in other regions. The systematic values of these endemic forms, variety, species, sub-species, genus, family and

consequently makes possible a conclusion as to the duration and completeness of the isolation.

Physiological isolation is due to mutations of the generative organs in such a way, the two groups lose their fertility. But geographic isolation does not need this help. Geographic races of lion and zebra are completely fertile.

These theoretic considerations of the *ROLE* of geographic isolation in evolution of species is amply supported by the facts of animal distribution. *Jordon's Rule.* "If we take a given species in a specified area as a starting point we do not kind its nearest relative in the same district: but in an adjuscent area separated by a banier. This is true of generally expanding animals.

eg; birds, insects, mammals.

Isolation is also seen in related forms living in different environments. This is *ecological isolotion.*

eg. Cambarus Monongalensis—found in springs with clear water. C. drognes found in stagnant water. Closely related forms which now inhabit the same area may of course have originated from separate areas and have migrated. The same barrier will be of very different effectiveness for different species.

Vagility: Vagility is the power of dispersal. The less the Vagility of the species the more its difficulty to overcome barriers. The more numerous are the areas which afford it the condition of geographic isolation for it the more numerous are the opportunities for independent Variation. The degree of Vagility in different groups of animals is in inverse proportion to the number of geographic races given by a particular area. eg; The crested lark '*Galeride*' cristata, a strictly resident form which ranges rarely far from a district forms an unusually large number of local races. The grey sea eagle scarcely varies with a nicely world wide range.

Widely distributed cirr;pedes tend to develop in to local races unless they are planktonic. In Germany species of beetles are represented by a single sub-species, but flightless beetles are of numerous species. An excellent example of the effect of geographic isolation with in a restricted area is supplied by the Achatinellidae of the Hawaiian isles. These tree snails occur in numerous wooded ravines which radiate from the valcanoe, thus being separated in the middle treeless tracts, each one has a sub-species of its own.

The same barrier may separate a whole group of forms from their relatives. The two faunae have a great similiarity of composition with out being exactly identical. They *Vicariate.* Such vicariation takes place in a large rate between the mammals of Eurasia and North America. *Ex:*

Evbrasia	*America*
beaver	beaver
red deer	wapils
elk	moose
rain deer	Caribou

The mammals of Kilimanjaro and Kenia exhibit vicariation, in squirrels, monkeys, Lemurs etc.

Adaptive radiation.

When a barrier is old and existing long, mutations accumulate and animals of the rare origin line in different environments. Different habitats come to be filled by different animals. The Australian region affords an excellent example.

Ex: The marsupials all occupy diverse habitats. Closely allied vicarious forms are likely to occupy the same ecological "niche". The charadrius forms a third of all fresh water fishes of South America filling all sorts of of habits. The South American bird the ovenbird (family Funaridae) shows a similar adaptive radiation

replacing birds of the most diverse families in other parts of the world. 55 genera of this family is now recognised.

The Auks and Penguins are analogous groups in the arctic and the antarctic seas. Bodies of water isolated for long periods may acquire similarly radiating forms etc; The crustaceam cumacea in Caspian Sea genus pseudocumais divided into thirteen different species, but, this is rare in the ocean.

Geographic Isolation in The Ocean

As a rule open ocean has few barriers. Species seen there are related to the depth of the Ocean, nature of the bottom and the surface temperature. Species multiply due to endemic ratio. The conditions are different in shallow water. There distribution is limitted by more numerous barriers. Therefore range of species are smaller and the number of species in each genus is larger. Geographic species and Subspecies in each adjuscent areas is developed.

Restriction in coastal water leads to specific transformation in the fishes also. Littoral Sharks and rays are scarce about Newzeland but form a number of endemic species. Even mere lack of Vagility for sessile or slightly movable animals without any special barrier, may afford sufficient variation.

Genetics and Evolution

The whole process of evolution is the result of a battle between random variations in gene frequencies, as a result of recombination and mutation and of the tendency of selection to fix in the gene-complex those allelomorphs which possess the highest adaptive advantage, and to eliminate those which are the least favourable. The result depends on the relative strength of the two forces. If the environment remained constant, all populations would attain a state

of equilibrium fairly rapidly, and a balance would be struck between selection and mutation and no evolution would occur. The environment is not normally stable, and such a state of equilibrium is extremely unlikely to be reached.

There is, however, another factor which is important in determining the spread of a gene: the size of the population. In very small populations the rate of evolution is slow because of the small amount of variation available for selective agencies. Again, in very large populations, evolution is slow, since there is a tendency for selection pressure and mutation-rate to reach equilibrium. An intermediate-sized population is more favourable for evolution than either extreme. It has been suggested that the most favourable condition for evolution is for a large population to be split up into smaller groups between which there is a certain amount of migration and subsequent cross-breeding. Exactly what is meant by a medium-sized population is at present not very clear. It is extremely difficult to measure, since what we need to know is not the total number of individuals, but the size of the effective breeding population, for the success of a particular individual, or group of individuals, depends on the number of offspring which it leaves. We have very little information about the magnitude of such a population. In general terms, a small population is probably of the order of a few hundred individuals and a medium-sized one of the order of a few thousand.

Another important aspect of population size is of a more dynamic character. A great many organisms are known to fluctuate in number rather rapidly, they may, for example, be reduced to an extremely small number during the winter months and multiply rapidly during the summer. This fluctuation of numbers is of real importance in the evolution of species.

When a mutation occurs in a rapidly increasing population it will be enabled to spread because the

selection pressure will be so low that even disadvantageous genes may spread through the population at this time. These genes, as a result of their spread, will be tried out in numerous gene-complexes with which they will react in different ways, and if one of the combinations is found to be beneficial it will be favoured by selection when the pressure increases again. When the population has reached its maximum size and then starts to decrease, all disadvantageous genes will be wiped out with great rapidity, whilst any advantageous combination which has arisen will be able to maintain itself. Fluctuations in numbers, therefore, provide an opportunity for the acceleration of the normal evolutionary processes.

It seems, then, that the sort of gene and chromosome differences which are seen to exist between species can spread through populations under certain conditions. Some explanation has been found for the divergence from one another of established species, or the spread of evolutionary trends within an interbreeding population. The splitting of an interbreeding population into two or more groups which no longer interbreed, the formation of new species, still requires explanation.

The origin of species seems to depend not only on the spread of genes through a population, but also on effective isolation of part of the population from the rest. Without isolation a species is not formed. Isolation can be of several kinds.

The most obvious type of isolation is geographical. Groups of organisms become separated from one another by mountains or rivers or some such natural barrier. If a lake containing fish were to become divided into two smaller lakes as a result of drought, then two groups of fish would be entirely isolated from one another, and no intercommunication would be possible. The two populations would not be able to interbreed and might evolve along divergent lines.

Isolation may be ecological, that is, two groups may come to frequent different habitats. In Switzerland there are two distinct races of the moth *Lasiocampa quercus*, one of which inhabits regions above 2,700 m., and the other, regions below 1,700 m. above sea-level, whilst a few hybrids occur between the two. The two races are fairly effectively isolated from interbreeding. The inhabiting of these different ecological niches may depend on a simple genetic difference, for example, adaptation of the two groups to life at different temperatures. A rather similar type of isolation which prevents interbreeding is seasonal isolation. Two groups of similar individuals are prevented from breeding together, because they mature at different times of the year. One species of the mollusc *Sepia* breeds in the spring on the Alantic and Mediterranean coasts, while the other species breeds in the same places at a rather greater depth and in the winter months. Two species of toads, *Bufo americanus* and *B. fowlerii*, inhabit overlapping territories: *B. americanus* breeds much earlier in the season than *B. fowlerii*, so that although hybrids do seem to exist they are rare. A different time of breeding could easily depend on one or a few genes which might alter the rate of maturation of the gonads. So far no direct analysis of these forms seems to have been made. Similar isolating mechanisms are found among plants. Certain species of *Iris* are known in which artificial crossing for experimental purposes is extremely difficult owing to a difference in the times of flowering.

Yet other forms of isolation are to be found in sexual isolation of various types. A slight alteration in the structure of the external genitalia of Lepidoptera would prevent copulation with members of the original type. The breeding behaviour may become different, so that members of one group are no longer stimulated or attracted by members of another. In plants the incompatibility mechanism discussed in an

earlier chapter falls into this category. The specialised flower structures of some orchids and some leguminous plants, for example, also seem to have originated as isolating mechanisms of this sort.

There are other types of isolation which may be effective, but which are, perhaps, less obvious. The hybrids between two species of flax, *Linum austriacum* and *L. perenne*, are normally incapable of germinating, so that the two species are effectively isolated. If, however, the seed coat is removed artificially from the embryos, they germinate and grow into fertile hybrids. *Drosophila melanogaster* and *D. simulans* can be crossed, but the hybrids so produced are sterile, and it has been found that gene differences exist between the two species which prevent the germ cells even beginning to undergo the meiotic division. Chromosomal rearrangements may in some cases also cause sterility. Individuals bearing translocations or inversions when crossed with the original type give hybrids of low fertility. In such cases, homozygotes for the rearrangement would presumably be viable and fertile, whilst the heterozygotes would leave far fewer offspring, if indeed they left any. Chromosomal rearrangement provides an effective isolating mechanism.

Polyploidy, which brings a new species into being at one bound will, in most cases, be an effective isolating mechanism. The new type is prevented from successful breeding with the ancestral species from which it arose, since hybrids are almost certain to be infertile owing to failure of meiosis. The formation of species by polyploidy is a rare phenomenon in the animal kingdom, though probably of considerable importance among plants, examples of which have already been considered.

Of all these isolating mechanisms, the geographical and ecological seem to stand first in importance. It would scarcely be expected that genes responsible for

interspecific infertility would spread within an interbreeding population, causing it to split into two groups. If such genes were present in the population they would lower the average fertility of the organisms carrying them, and hence the selective advantage of of these individuals would also be lowered. It seems likely, therefore, that populations become isolated by some geographical barrier or by ecological isolation, while otherwise still capable of interbreeding. Once they have become effectively isolated in this way, gene differences may accumulate which are not in any way disadvantageous within the group, but which lead, for example, to infertility or lack of sexual attraction between individuals of the two groups. Following on gene differentiation, or concomitant with it, may come the accumulation of chromosomal rearrangements, such as inversions or change in total chromosome number, so that the two groups differ from one another in numerous and complex ways, A subsequent breakdown of the geographical or ecological barrier would allow free intermingling of the groups, but they would be isolated effectively by gene and chromosome differences. Thus in the formation of species it seems that some extraneous factor is necessary for preliminary isolation, but once this has been achieved, isolation may be taken over by genes and chromosomes, so that the groups remain isolated, in the sense of not interbreeding, even when the initial barrier is broken down.

An attempt has been made to indicate the ways in which species have originated from one another and have been perpetuated (micro-evolution); but nothing has been said of the evolution of large groups such as orders (macro-evolution). There is no experimental evidence available to show how the main evolutionary lines have become established, and some authors have maintained that a process is involved which must be fundamentally different from that which appears to be responsible for the origin of species.

It seems unnecessary to invoke a new mechanism until the available one has been proved ineffective, and this is by no means the case. Over the millions of years which have been available for evolution, gradual divergence by means of accumulated gene and chromosome differences seems adequate to account for the process, particularly when it is remembered that different groups of organisms have had different rates of evolution.

The sceptics demand the production of all intermediate types of organisms if the mechanism of speciation is to be accepted as the basis for all evolution, and this has clearly not been done except in a few notable cases. There are several possible explanations of this seeming failure. It is self-evident that many ancestral types would not be preserved as fossils, either because they had no hard skeletons or because they did not inhabit an environment which was suitable for their preservation. Secondly, there are clearly many more fossils in the rocks than man has succeeded in finding. Thirdly, some evolutionary advances may have been more drastic in their phenotypic effects than we have envisaged even though involving comparatively minor gene changes. The mutation of a gene with far-reaching effects, working early in ontogeny, if it were not disastrous to the organism might bring about an evolutionary leap, and no intermediate types need be sought. The invocation of neoteny to 'explain' the evolution of the chordates from echinoderm ancestors would fall into this category.

Lastly comes perhaps the most important point, and one which is usually overlooked. Major evolutionary advances have frequently been brought about in response to the opening up of a fundamentally new ecological niche. For example, the Amphibia, attaining the land, had a sparsely populated habitat to colonise with practically no predators or competitors. The

initial population which established itself in this new habitat could have been very small, but it would presumably have expanded with great rapidity, since selection pressure would be low. This rapid increase in numbers would be likely to result in a population of great variability, a quality which would persist until the selection pressure increased and the numbers became stable. During this sudden rapid expansion, the main groups of Amphibia could have come into existence. In cases like this, where a very small stock gave rise rapidly to a large and variable population, it is improbable that fossilised remains of the small initial colony would be found, and those individuals of the expanding population which were unearthed would probably be assigned to different genera, families or even orders.

There seems, then, no reason to assume that macroevolution is fundamentally different from microevolution, but rather to suppose that all evolution has come about by the accumulation of nuclear and cytoplasmic differences under the pressure of the changing environment.

Mendelism and Selection

E. B. Ford is a Neo-Mendelian. This essay is from his book 'Mendelism and evolution'.

We have now reached two important conclusions, that the results of experimental genetics may safely be applied to the solution of evolutionary problems in nature and that the great bulk and perhaps the whole of organic inheritance must be of the Mendelian type. These enable us to draw certain deductions from the facts so far considered. We have seen that genetic factors interact with their internal environment and that their effects can in consequence be altered by selection operating on the gene complex. It is evident that such selection opens up another possibility of considerable importance for evolutionary theory; that the effects of a given gene may gradually alter. We have in fact no ground for assuming that the characters which a particular gene gives rise to are those which it produced at its first appearance. We are therefore confronted with two distinct effects of selection which have not generally received separate recognition. First that an inherited character conferring any advantage on the individual will tend to spread through the species since the individuals which possess it will be favoured by Selection. Secondly that the effects of a gene if advantageous may be intensified and perhaps altered in quality, owing to the tendency for those individuals to be preserved whose gene complex brings them out to the greatest extent.

The first of these processes, the natural selection of characters is of course familiar to all Students of biology and has gained general acceptance. It is not seriously doubted that individuals possessing any specially advantageous character will on the whole contribute more to the ancestry of future generations than which fall below the average standard of the species and that in so far as such departures from the

mean are inherited, this process will lead to evolutionary change. This is pure Darwinism and assumes no special type of inheritance. The second, the natural selection of factors is one which follow inevitably from such facts and is the out come of Mendelian research. It will be found to remove some of the difficulties felt by those who hold that the principle of particulate inheritance are at variance with what is known of evolutionary progress.

These difficulties are of several kinds but they may perhaps be grouped under three main headings. Two of these have already been discussed. The third is due to the idea that the characters controlled by Mendelism arise ready made by mutation to be selected or rejected in the struggle for existence as the case may be. Such a discontinuous origin of characters is in its crudest sense rightly felt to be inconsistent with the slow and continuous course of evolution. This objection has been stated clearly by prof. Mac Bride, who says, "Suffice it to say that this doctrine......... finds no countenance with those really competant to speak on the subject of evolution. Our leading systematists, palaeontologists and embryologists are all convinced that evolution has been slow, functional and continuous."

It is to be noticed that this criticism omits all reference to an important condition of the theory, the size of the mutational steps involved, clearly if these were very small, almost continuous evolutionary progress could result, that many genes which become incorporated in the species have arisen by mutation. It is however well known that many genes do produce striking effects and to these the criticism now under-discussion might at first sight seem to apply. It is to be noticed, many such genes are successful and have been able to establish themselves in nature; among many other forms the Lepidoptera especially those displaying mimetic resemblances show numerous clear

instances of this. In Papilio Polytes, papilio memnon and the genus Hypolimnas, for example polymorphism involving the most striking changes is certainly controlled by single factors. It may then be inquired how adaptations such as these have been brought about.

We would of course agree with prof. Mac Bride that it is quite unthinkable that mutation after mutation could have appeared at last are happened to hit off the wonderful resemblance which we see between mimic and model in these insects and this could have happened repeatedly in a great number of species. As pointed out a few years ago by Fisher, the solution is probably to be found in the interaction of individual genes with the gene complex, in the manner already outlined.

We have no reason to assume that when genes such as these first appeared their effects were similar to those which they produce today. On the contrary we may suppose that in a given palatable species a gene arose which chanced to give some slight resemblance to a protected form. This would gradually be improved by selection of one gene complex until an accurate mimicry had been attained.

It will thus be apparent that though genetic factors have their origin in spontaneous mutation, this does not in the least imply that the characters which they control are not susceptible of slow and continuous evolutionary change.

This is a conclusion of considerable importance. It is of course an extension of the theory of dominence which was discussed in the last chapter, and it is evident that an advantageous gene will become completely, dominent in the manner there described, at the same time that its effects are being improved. There is of course no need to assume that such a gene possessed any advantage from the outset. Initially

disadvantageous and virtually non-adaptive genes may ultimately become established through environmental changes. A character which is of no advantage at one period is useful at another, while the recurrent nature of mutation allows the genes to make repeated bids for success.

It is evident that domestication, with its artificial selection will greately increase the rate at which genic improvement can take place. They have indeed been detected even at the present time. For *eg.* the fish 'Labistes reticulatus' has for many years been bred in captivity for aquarium purposes. The males are polymorphic and Winge finds that the various forms are often more 'beautiful' than those to be obtained in the wild state suggesting that appreciable modification has been brought about by human selection. Winge was himself able to show that the effects of one of these genes that is known as maculatus could definitely be altered by selection.

Although in natural conditions such processes as these are most likely to place over long periods of time during which considerable changes may be expected in the environment. It has been established by Elton, that fluctuation in numbers is a phenomenon of wide occurrence in animal communities. He has therefore pointed out that the opportunity for the spread of genes which fluctuation provides may be an important factor in evolution.

It is apparent that when a mutation chances to occur in a population which in rapidly increasing, it will be enable to spread in a way which would be impossible if the numbers had remained constant and each pair had on the average been giving rise to but a single pair in the next generation. Practically non-adaptive genes would thus be placed in a number of different gene-complexes. Should one ot these chance to be beneficial, the effect so produced would be

favoured by selection. This would lead to the establishment of such a gene and of the gene-complex with which it reacted usefully. Any advantageous combination could have arisen would however maintain its pooling at this time and lead to an adaptive change in the population as a whole.

Fluctuation in numbers may give an opportunity for normal evolutionary processes to take place more rapidly. For so long as the numbers remain constant the rate at which a non-adaptive, character can spread is so exclussively slow as to be almost negligible, while the opportunities for recombination accorded to a disadvantageous gene must be small indeed. It would appear, however that in general an evolutionary change will only take place if an advantageous variation results from this process. The chances that the particular individual in which a non-adaptive mutation occurs should be the ancestor of an unduly large proportion of a subsequently increased population are very remote, that is if no improvement occurs in the effect of the gene.

There is strong probability that the effects of the genes are multiple. This consideration must throw some light on the nature of the characters which separate local races and closely allied species.

It is known that certain genes which have beneficial effects may at the same time produce characters of a non-adaptive type, which will therefore be established with them. Such characters may some times serve most easily to distingiush different races or species. Further it may happen that the chain of reactions which a gene sets going is of advantage, while the end product which gives rise, say, to a Character in a juvenile or the adult stage, is of no adaptive significance.

J. S. Huxley has pointed out another way in which non-adaptive specific differences may arise. For he

has shown that changes in absolute body size in themselves probably adaptive may automatically lead to disproportonate growth in a variety of structures such as horns and antlers in mammalia and the appendage in Arthropda.

It is not perhaps always recognized how complete has been the characters available to systamatists for the separation of allied species may be of a wholly non-adaptive kind.

It has been shown by Fisher that the necessary condition for the establishment of polymorphism of the Mendelian type is first that the ratio in which the members of alleiomorphic pair occur should be in stable equilibrium. That is to say if for any reason their proportionate numbers are disturbed, they will tend automatically to return to their original value. Secondly that no such stable equilibrium as this could be maintained in the absence of selection. The truth of these two proporitions will be evident from the following consideration.

Two types of equilibrium therefore are possible, polymorphism will result if the heterozygote possesses some physiological advantage as compared with the homozygote. It would seem improbable that such a condition such as this is often maintained with out other contributing factors as improvement in the fertility of the more favourable homozygous type must be expected to take place. It may on the other hand be controlled by the nature of the advantage itself. Thus a Batesian mimic will progressively lose its advantage as its numbers increase relative to those of its model, untill its necessarily conspicuous pattern actually become a danger. If polymorphism exists in such a species the numbers of the different forms will be adjusted untill each receives equal protection. Optimum proportion would thus he arrived at in any given locality departures from which in either direction would constitute a disadvantage. In such a situation

as this no form would be able to spread completely through the species. It is to be noticed that polymorphism is in fact common in mimetic insects.

These two forms of stabilizing action may be combined. Fryer encountered numerous sterile unions in his 'polytes' and it has been pointed out by Fisher that the simplest explanation of this is a reduced fertility of a homozygous mutant type. The part played by physiological agenencies may further be illustrated by the polymorphism studied by Gerould in butterflies of the genus colias.

The stable nature of the equilibrium which characterises polymorphic species is further indicated by the fact that it may some times persist for long periods of time. It is evident however that where stability depends upon ecological factors, the proportions of the different forms may vary widely in different localities. Stability may further be upset or rather it may have a slightly different meaning if the species concerned is one whose numbers are given to fluctuation. For the whole ecological situation may be different when the population is at its maximum and at its minimum.

From what has been said of dominence it will be evident that in all types of polymorphism the heterozygote will come to resemble the more advantageous form though in the homozygote this may be counter balanced by some genetic disadvantage. Thus the white females of the genus 'colias' studied by 'Gerould' are dominent though they are the raver form in nature. In ordinary circumstances we should expect on an advantageous and therefore dominent gene to have spread out rapidly throughout the whole species. The condition of the homozygote prevent this. The heterozygotes will therefore be particularly quiet to convert themselves to the more advantageous type.

Haldane has drawn attention to those curious instances in which polymorphism in nature is associated.

with close linkage either between genes or whole chromosomes and with the occurrence of a relatively common "universal recessive". It has already been suggested that the close linkage and frequent allelomorphism which occurs in species is due to linkage between whole chromosomes and it is accounted for by sectional translocations, the dominent genotype being due to duplication of such translocated segments (Haldane). Fisher has pointed out that this is probably balanced by a defficiency in viability associated with the homozygous duplication. He has actually been able to demonstrate a significant defficiency of homozygous dominants in Nabour's extensive breeding experiments on locusts.

Fisher points out that where close linkage exists the number of recombinations available for genic improvement is reduced. In these circmstances the genes no longer compete with their allelomorphs independently in pairs but large systems of linked genes, or perhaps entire gene types, come in to competetion as if they were a system of multiple allelomorphs. Many genes which confer only a selective advantage thus be continually crowded out. A character involving only small selective advantages such as colour-pattern, may thus be debarred from the main method of evolutionary adaptation. This allows a duplication or other chromosome abnormality deleterious when homozygous to improve the colour pattern and establish polymorphism. For the dominence of such factors could not be developed by the selection of modifiers as these would enjoy a still lower selective advantage. Duplications however provide a tract of chromatin in which as heterozygotes these less important genes may be modified by selection while they are protected from the competition of the universal recessive gene complex.

The Gene Theory and Mutation

The gene theory :— The name gene was applied to the hereditary unit by Johansen with the intention that it would be just a convenient term to designate the units of heredity, which Mendel had referred to as 'factors' or 'elements'. He stated that he proposed this term without intension of implying any particular theory of the nature of the hereditary units. The name has become closely associated with the theory of T. H. Morgan, that the genes are corpuscular bodies in the chromosomes arranged in linear order like beads on a string. Each gene separated from all of the others and different from all of the others in substance, while all of the genes of a particular chromosome are held together by an indifferent substance This theory in based upon three types of evidence: the fact of the mutation, the fact that a linear order of genes in the chromosome can be established by cross over tests ; and the fact that once this order is established, it can be reshuffled by subsequent crossing over.

This morphological concept of the gene dominated genetic thinking for many years. Its boundaries were soon blurred by position effects and most recently investigation of the biochemistry and physiology of the gene have increased the difficulty of setting exact boundaries to it — so that physiology rather than morphology dominates current thinking about the gene.

Gene number and gene size :—

Attempts have been made to estimate the number of pairs of genes for various organisms. Obviously a direct estimate of the number of genes is not available for any organism both because a complete study of all hereditary characters of a single organism has never been made and because a particular gene is identifiable by genetic methods, only when it is available in more than one form, in other words when it has mutated to

form two or more alleles. Estimates for Drosophila melanogaster genetically the best known organisms, range from 6000 to 15000. Belling has estimated about 2200 genes for 'Lilium'! And 'Curt Stern' estimated not less than 5000, nor more than 120,000 for man.

Estimates of the size of the gene are based upon the volume of the gene are based upon the volume of the chromosome divided by the estimated number of genes. On this basis Gowen and Gay calculated the average size of the genes of Drosophila to be 1×10^{-18} cubic centimeters. More recently Pease and Baker using the electron Microscope, have abserved the salivary gland chromosomes of desophila leaf shaped be die? which they believest to be the genes. These vary in size but the average is about 1×10^{-17} Cu. Cms. As the Salivary gland chromosomes are grant chromosomes to begin with the mere fact that these bodies are ten times the size estimated by Gowens and Gay can not be regarded as conflicting with their estimate. But neither is there any preof that these bodies actually are the genes. If the boundaries of the gene are actually indefinite then the significance of such estimates is considerably reduced.

Whatever their nature then there is very abundant evidence that the genes do mutate that this is a source of variability which must be studied for its bearing on evolution. A mutation may be defined as a permanent change in a gene. Alleles exist only because the original wild type gene has mutated at the same time. Like the original gene the mutant is recognized by the character which it causes.

Mutation. A gene which is responsible for producing normal red eyes in Drosophila melanogaster has an allelomorph, white, which affects the developmental processes in such a way as to produce a change in the type of pigmentation of the eyes. Allelomorphs may exist in two or more states, giving rise to contrasting

effects in the characters which they control. A herditary variation such as white can arise from a wild type gene complex. Many such variations have been observed to do so in wild stocks kept in the lab : and they have also been reported occasionally from the field. This inception of a hereditary variation or change in any unit of heredity is known as a mutation. A mutation is a sudden event, the mutation to white eyes in Drosophila for example occurred suddenly and in one step. In one generation of all the individuals had red eyes and in another an individual appeared with white eyes. There was no gradual change from red through various shades of pink to the final white.

Darwin described examples of mutation but was unable to interpret them in the modern may since he was unaware of the law of inheritance and of the existence of the chromomes and genes and he is of the opinion that the material of natural selection was mainly called forth by the environment.

In 1889 the Statistician Batton and in 1894 the biologist 1889 Bateson showed that variations are frequently incontinuous and they believed that such variation appearing as new steps were the chief building blocks on which natural selection could operate. Between 1901 and 1903 Devries profounded his mutation theory.

Since the begining of this century mutations have been investigated experimentally and evidence as to the nature of these mutations is accumulating steadily. Something is known of the way in which mutant genes differ in their mode of action from that of their wild type allelomorphs, and the mutation rate of genes can be increased by artificial means but as yet it is not possible to give an exact definition of a mutation. The best definitian seems to be that a mutation is the inception of a heriditary Variation.

If this definition is accepted mutation can be of two sorts if it may be the result of a change in the total number of the chromosomes or it may be genetic, that is a change in the nature of one gene. To describe a change in chromosome constitution the word is usally qualified to read chromosome mutation.

In 1927 Muller discoverd that if he X-rayed Drosophila individuals in gelatine capsules at doses which were just sub lethal, he was able to increase the mutation rate by about 1 to 50 times. Temperature and ultra violet rays increase the rate slight and recent works show that certain chemicals also have an effect. Mutations have been induced by artificial means in about 50 different types of plants and animals from protozoa upwards.

As a result of extensive work Muller came to some very important conclutions about the effects of X-rays.

1. He found that all the mutations he produced artificially were similar to those occurring spontaneusly and that of these mutations there were ten to fifteen times more lethals and nonlethals. Mutations occurring spontaneously seem to be far more often lethal than not. This is scarcely surprising since the gene complex is a very finely adjested system and any violent change would probably cause too much upset for the system to be able to work. Another point which mnst be considred is that the organism that are being subjected to experimental work have been in existence for a very long time and during this time. They have had opportunities to try out many mutations. Natural selection probably weeded out those mutations which were of the value to the organism in its particular environment. If this is the case it is not surprising to find that many of the mutations which occur are disadvantageous when compared with the wild type.

2. There is a different degree of mutability of individual genes, 'Artificial' mutation rates are proportional te the rates for sportaneous mutations, for example, the dark allelomorphs of the white eye locus of drosophila mutate more frequently then the paler ones.

3. Mutations can occur in any cell of an organism and are not confined to the germ tract, though obviously it is only those occurring in the germ cells which can be passed on to subsequent generation. The production of mosaics in which are or a few somatic cells show a mutation is more easily brougt about in plants than in animals. The white specks on the leaves of variegated plants are some times the result of somatic mutation.

4. There is no after-effect of the irradiation. That is to say, that if a normal chromosome is introduced in to X-rayed cytoplasm, the cytoplasm does not affect the chromosome. If unfertilised eggs of the hymenopteron, Habrobracon are exposed to very heavy doses of X'rays the chromosomes break up and cease to function. No effects of the radition were delected on the introduced male chromosomes. It appears from this that the X-rays act directly on the chromosomes or the genes themselves and not through some indirect effect as, for example causing chemical changes in the cytoplasm which in turn induce mutations in the genes.

5. It is possible to produce reverse mutations. For ex. irradiated flies have given rise to offspring with forked bristles. In the course of time under X-ray treatment flies have shown sudden returns to the normal type and at a later date still have reverted back to the forked type and so on. It frequently happens that it is more difficult to induce to reverse mutation, than the original or vice versa. On the other hand, the fact that reverse mutations can take place

shows that a mutation is not the mere absence of a gene but must be a change in the nature of the gene.

6. Muller found that there is a direct proportion between the dosage of X-rays and the number of mutations produced. There is a linear relationship between dosage and mutation-rate, an important conclusion.

7. The time factor is not important. It makes no difference to the mutation-rate whether the does is intense and the exposure time short or the radiation weak and the exposure time long if the total dosage is the same in both cases.

8. The mutation rate is independent of the wave length of the X-rays used. This is true for all wave-lengths from γ-rays to very soft X-rays and also β-rays.

The conclusion is then, that the linear proportionality of the mutation rate to the total dosage given is independent of any other characteristics of X-rays. A short exposure to intense radiation is no more effective than a longer exposure to weaker radiations. The fact that the relationship is linear indicates that a mutation is caused by a single event and since it is independent of other variables, it seems as though the single event must be an ionisation. The types of X-rays which are used produced a scattering of ionisations fairly throughout the tissues but this is not the case with α particles and neutrons. These rays produce ionisations and if mutations are dependent on ionisations we should expect to get fewer mutations with these rays because of the wastage of hitting a single gene twice.

Mutation in nature. Critics of genetics long held that the mutants with which geneticists worked could not be significant, because such mutants were not a really natural phenomenon, but a sort of degenerative effect of laboratory environment. This has been

abundantly disproved investigators have found in nature many mutants identical with or similar to those dealt with by laboratory zoologists. The original drosophila mutant (white eyes) was as a matter of recored captured in nature by the entomologist 'Lutze' at about the same time that it arose in the laboratory stocks of T. H. Morgan. Goldschmidt found many mutants found in the wild populations of drosophila near Berlin. Dubinin collected the same species in several localities in the Caucasian Mount ains. On inbireeding he found that the incoldence of lethal genes varied from 0 to 21.4% in different localities, while visible variations varied from 3·9 to 33·1%. Many of these had minor effect. Baur studied wild snap-dragons and found that about 10% of the plants showed atleast one mutant. Dice has found that wild populations of the deer mouse Peromyscus always have many mutants. It may then be regarded as established that mutation is a normal phenomenon in nature.

Ultra-violet light increases the mutation-rate under experimental conditions and organisms are constantly exposed to it under natural conditions. The difficulty is that ultra violet light has an extremely low penetrating power and is unlikely to reach the tissues under normal conditions.

The only other agencies which have so far proved effective are a few chemical compounds when Drosophila adults are exposed to mustard Gas Vapur for a short time the mutation rate is increased considerably. Parallel results have been obtained with a dilute solution of phenol. Gonads of larval drosophila soaked in a solution of .01% phenol for a short time and then planted in host lavae, give rise to offspring bearing more mutations than would be expected from a knowledge of the normal mutation rate. Although This recent work is very suggestive it must be admitted the cause of naturally occurring mutations is not yet known.

The mutation rate of all genes is extremely low. At first sight it might seem as though it was too low to be of any importance; but if mutations were occurring all the time there would be no stability in the gene complex. The low frequency of mutations allows them to be formed out one at a time and tried out in the force of natural selection. It is desirable to preserve in the genetic make up those that are advantageous. The low mutation rate allows just enough change for trying out new efforts without upsetting the optimum stable gene complex.

A point which has not so far been raised is the meaning of a given mutation rate. The absolute mutation rate of Drosophila which completes an entire life cycle is less than three weeks, could scarcely be expected to be the same as the mutation rate of an elephant or a man which requires years for the same purpose. If the mutation rate in man were the same per unit time as in drosophila there would be an accumulation of mutation in the sperm, so that all spermatozoa would carry mntations most of which might be expected to be lethal and disastrous to the species. It is probable therefore that mutations ought to be calculated as the number per life cycle. Probably some kind of adaptation of the mutation rate takes place in relation to the length of the life cycle of the particular organism.

Muller has suggested recently that the mutation rate is also influenced by the length of x chromosome. In the haterogametic sex all mutations occuring on the x chromosome, whether dominent or recessive, are exposed to selection. If there are many genes on the x chromosome and the mutation rate of the organism is high too many deleterions mutations will appear for the species to be sucessful. Specific genes are known too which themselves affect the mutation rate and in some slowly developing organisms those genes which slowed down the mutation rate would presumably be favoured by selection.

Chromosome mutations

Or

Changes of the Chromosomes

In the last chapter mutation of the gene was considered, although at the beginning it was made clear that there are other types of changes which comply with the definition of mutation: the inception of a hereditary variation. It is these other changes, changes in the structure of the chromosomes which form the subject of this chapter.

Two main classes of chromosome changes can be distinguished: (1) structural changes which alter the arrangement of the genes or the actual number of genes in the chromosomes; (2) numerical changes which increase or decrease the total number of chromosomes.

Chromosomal rearrangements can be brought about artifically by treatment with X-rays, certain chemicals and by exposure to a sudden extreme of temperature. How these rearrangements are brought about under natural conditions is not at all clear. and little is known of the frequentcy with which such changes occur. The first deficiencies, duplications, translocations and inversions detected in *Drosophila melanogaster* were spontaneous in origin, all though, of course, so-called spontaneous rearrangements may, in fact, be brought about by some external catastrophe.

For quantitative work on the nature of chromosome rearrangements we must again turn to the work of Muller on the effects of X-rays. Muller found that, just as with gene mutations, the time over which a dose is given and the wavelength used is unimportant. When rays are used which have shorter wave-lengths than X-rays the same proportion of structural changes produced long wave-lengths as with genemutations.

Therefore it is only the total dosage of X-rays which matters. The relationship between dosage and chromosome mutation, however, is not a linear one but gives a ratio of 3 : 2. On purely theoretical grounds it would be expected that if, as seems likely, chromosome mutation is dependent on two events, the breaking of two chromosomes or parts of chromosomes and their subsequent rejoining, a square ratio would be found. The departure from this expected ratio is probably the result of the occurrence of multiple breaks instead of only double breaks and a rejoining, in some instances, of the original ends.

On experimental evidence we can say, therefore, that, whereas gene mutation depends on a single event, chromosome changes seem to depend on a double event. Under the influence of X-rays then, chromosomes can undergo fragmentation and the fragments can rejoin in different ways or be lost altogether.

It seems likely that broken ends have a tendency to join with other broken ends rather than to attach themselves to the natural end of a chromosome. Chromosomes with broken ends seem to be unable to survive for long periods unless they can become re-attached. Consequently, the existence of such chromosomes leads to the death of the cell. Chromosomes with natural ends seem to be able to exist indefinitely.

A study of the fragmentation of chromosomes has shown up very clearly the importance of the centromere. Fragments which become broken off and fail to rejoin and which do not include the centromere in their meterial are incapable of taking part in the mechanics of cell-division. Alternatively, if, as a result of brakage, two fragments both possessing centromeres join together, they may become stretched on the spindle owing to the pulling of the two centromeres in opposite directions until eventually the fragment breaks under the strain.

(1). **Deficiency.** A section of a chromosome containing one or a block of genes may be broken or lost during a nuclear division If a normal chromosome is made up of genes *ABCDEFG*, a deficiency might occur as the result of the loss of section *FG* Crossing-over does not take place in a deficient region, which suggests that this part of the cross-over map is really absent.

It is in this context that the importance of the salivary gland chromosomes of the Diptera becomes apparent. Since a detailed map exists of the arrangement of all the bands on these relatively huge chromosomes, even a small deficiency can be detected, and similarly with other types of structural rearrangement.

In the homozygous condition deficiencies are usually lethal, and in the hetrozygous state they are frequently so. Probably the viability of heterozygotes can be coorelated with the length of the missing section, although some genes do appear to be more easily dispensed with than others. It seems likely that 'lethal gene mutations' are quite frequently minute defieiencies.

(2). **Deletion** is the name given to large deficiencies which are interstitial in the chromosome. They were so called to distinguish them from deficiencies which could be terminal. It is doubtful, however, whether deficiencies are, in fact, ever really terminal.

(3). **Duplication.** A section of a chromosome may be present in an unusual location as well as in its normal position. For example, chromosomes of the constitution *ABCDEFG* and *WXYZ* may have the section *FG* duplicated and attached to the chromosome *WXYZ* as well as being present in the normal position, An individual bearing this type of rearrangement has the genes *F G* represented three times.

As example of a duplication which seemed at first to be a gene mutation was found in the *X*-chromosome of *Drosophila*. The condition *Bar* eyes, which is dominant, depends on a very short duplication in this chromosome which can be seen by a study of the salivary gland chromosomes. The manifestation of *Bar*, a reduction in the number of facets in the eyes, is only brought about by the presence in triplicate of this particular region *X*-chromosome In a female one chromosome has the region present once, whilst its homologue has a double doses as a result of the duplication of this region. It has been suggested that duplications might be the source of new genes in evolution. If owing to a duplicatio n, a particular gene is represented three or four times in the gene-complex, one of the loci might mutate whilst the others remained unchanged. Furthermore, a mutation of, say, two genes out of a total of four might not be physiologically disastrous, and could be preserved where otherwise it would have proved lethal. Extensive studies of the salivary gland chromosomes of wild *Drosophila* populations have shown deficiencies and duplications to be very rare in the field. However, in another dipteran *Sciara*, quite a large variety of these structural alterations has been reported from wild populations.

Other structural changes in chromosomes do not alter the amount of chromosome material present, but alter the normal arrangement of thr material.

(4). Translocation is one way of rearranging the available chromosome material. A fragment of a chromosome may become broken off from its normal place and attached either to another chromosome or to a different region of the same chromosome. Thus, by translocation. chromosomes *AFG* and *WXBCDEYZ* could be obtained or the two original chromosomes might exchange parts to give a reciprocal trans-

location and the new chromosomes *ABCDEXW* and *GFYZ* As a result of such a translocation entirely new linkage groups are formed.

Translocations can be detected cytologically in the salivary gland chromosomes and often also in metaphase chromosmes, where a typical ring formation can be seen Individuals heterozygous for translocations produce some gametes bearing duplications and deficiencies. In an individual of the constitution represented in Fig. at least the following typs of gametes could be formed: (1) *ABCDEFG, WXYZ*, which would be normal; (2) *ABCDEXW, GF YZ*, which bears the translocation, but in which all the genes are represented once; (3) *ABCDEFG, GF YZ*, which is deficient for *WX* and has *FG* represented twice; (4) *ABCDEXW, WXYZ*, which is deficient for *FG* but has *WX* represented twice. In animals the gametes bearing duplications and deficiencies either die or give rise to inviable zygotes, and in plants the affected part of the pollen or ovules aborts.

Translocations are very rare in wild populations of *Drosophila*, but there is a certain amount of evidence for their presence in the scorpion, *Tityus*. Since translocations tend, in the heterozygous condition, to deminish the fertility of an organism they would be unlikely to establish themselves in wild populations. Translocations are known to occur in plants, and the problem of *Œnothera* must be considered, since it was the work of de Vries on this plant which first gave rise to a definite theory of mutation. Recent work has shown that *Œnothera* is pecular in having a large number of translocations in its chromosomes. Varieties of *Œnothera* breed more or less true when self fertilised, but produced a certain amount of bad seed and about 2 percent of types unlike parents, which are the mutants described by de Vries. The species contains chromosomes of two complexes, and these de Vriesian mutants are probably due to a segmental interchange

between chromosomes either of the same or of different complexes. Metaphase chromosomes of *Œnothera* show the typical ring formation associated with translocations

(5). The final type of structural rearrangement to be considered is an **inversion**. A fragment of a chromosome may break away and rotate through 180° before it re-attaches itself at the point of breakage. The resulting chromosome is made up of the same genes as the original, but they are in a different order. An inversion of section *BCDEF* would give the chromosome *AFEDCBG*. At meiotic pairing the homologous genes attract one another to such effect that the chromosomes form a loop. In hybrids or *Drosophila melanogaster* ~~and *D simulans*~~ a large inversion loop can be seen in Chromosome III.

Inversions can be detected in the salivary gland chromosomes of the Diptera, and can be suspected from breeding experiments, since they reduce the amount of crossing-over which takes place in anindividual heterozygous for the inversion. It is this effect of reducing crossing-over which may account for their very wide occurrence in wild populations of *Drosophila* If an inversion involves several genes advantageous to the species, it will, by the suppression of crossing-over among these, prevent the combination from being broaken up. In this way inversions have a positive selective value. Individuals homozygous for an inversion exhibit the normal crossover frequency.

One interesting fact that has emerged from a study of structural changes is that the functioning of some genes, at any rate, depends on their position in the chromosome. By altering the position of such a gene, its properties can also be altered. This phenomenon is known as the **position effect**. The condition *Bar*, as we have already seen, depends on a duplication of a short region of a normal *X*-chromosome,

and the *Bar* eyes in females are due to the presence in triplicate of this region. A more extreme condition known as *Double-Bar* or *Ultra-Bar*, has arisen, in which the eye facets are even more strikingly reduced. It has been found that in *Double-Bar*, the *Bar* region is present three times on the same chromosome Flies which are homozygons for *Bar* (that is, two *Bar Bar* regions on each chromosome to give a total of four *Bar*) and flies heterozygous for *Double-Bar* (that is, three *Bar* on one chromosome and only one on its homologue, again giving a total of four *Bar* but differently distributed) do not show the same reduction in the number of eye facets. In fact, the heterozygous *Double-Bar* has appoximately fortyfive facets compared with the homozygous *Bar* with approximately sixty-eight facets (wild type 780 approximately). Thus, extra *Bar* regions seem to have a stronger effect when situated on the same chromosome than when they lie on different chromosomes. It might be suggested that, in fact, gene mutation had taken place to produce this effect; but experiments with other genes susceptible te the position effect show that when such a gene is returned to its normal position it takes on its original properties once more.

It has been suggested that all gene mutations are really the result of inversions and translocations of a size so small as to be undetectable even in salivary gland chromosomes, the change in properties of the gene being due to the position-effect phenomenon. This seems unlikely, however, since it would limit the number of possible mutations condiderably, for an indefinite amount of rearsangement is not possible. In addition to this, it should be made clear that no instances of a position effect have ever been recorded outside *Drosophila*, although numerous inversions and translocations are known in maize.

The second class of chromosome change is concerned with numerical changes. Whole sets of chromo-

comes may be present in more than the diploid number, a condition known as **polyploidy** (*polys*, many + *eidos*) or less than the diploid number, haploidy, or individual chromosomes may be present in excess in an otherwise diploid complex, an arrangement to which the name **polysomy** (*polys* + *soma*) has been given.

First there may be a reduction in the total number of sets of chromosomes. The chromosome number is halved, giving rise to haploid individuals. It is intsresting to record that no haploid *Drosophila* has ever been produced, although flies are known which have patches of haploid tissue in an otherwise diploid individual. In these cases, the haploid tissue is always of the female type.

Secondly there may be an increase in sets of chromosomes. The normal diploid organism contains two of each kind of chromosome, except perhaps the sex chromosome, but chromosome complexes are found, particularly in plants, In which each chromosme is represented three, four or even more times and such organisms are known as **polyploids.** Polyploids may arise in two ways. A **tetraploid** (*tetra*, four + *eidos*) may arise by the doubling of the chromosomes of an otherwise normal organism, and the pelyploid thus produced is known as an **autopolyploid** (*autos*, self). Alternatively, a hybrid organism, in which the two basic sets of chromosomes are not indentical, may undergo doubling of the sets to produce a polyploid which is known as an **allopolyploid** (*allos*, other or different). The field garlic (*Allium*) is a naturally occurring autotetraploid, whilst *Galeopsis tetrahit*, the common hempnettle, is an allotetraploid derived from the hybrid of the cross *G. pubescens* × *G. speciosa*. The few well-authenticated animal polyploids all appear to be autopolyploids.

The phenotypic appearance of an autopolypoly-ploid is not usually very different from the original type, except that, in a number of cases, there is an increase in the size and vigour of the organism. This is probably dne to an increase in size of the individual cells as a result of keeping the ratio of cytoplasm to nucleus constant.

Cytological analysis of an autopolyploid shows a curious, though not unexpected, configuration of the chromosomes at meiosis. All the homologous chromosomes of one type may come together in a compound during this division, but the approximation of the chromosomes remains strictly in pairs at any one place, the compound mass, being formed by pairing together of different couples at different places along the length of the chromosomes. The result of this abnormal pairing is a reduction in the number of chiasmata formed, and consequently the homologues are not held together very firmly at metaphase, and segregation is frequently irregular. This abortive meiotic division leads te a high rate of infertility among autopolyploids.

Allopolyploids, which are formed by duplication of the chromosomes of a hybrid organism, are usually intermediate in general appearance between the two ancestral types. Examination of cells undergoing meiotic division shows that these polyploids are not always confronted with the same problem as the autopolyploids. The tendency to form a compound body at zygotene is not found when the two sets of ancestral chromosomes are rather dissimilar. There is no general paring up of four homologues, since they are not sufficiently alike. Instead, each chromosome pairs with its own homologue, and segregation can be abnormal as in the more usual diploid organism. Allopolyploids, then are more often fertile than are autopolyploids.

Polyploids originate by a partial failure of cell-division. Failure may occur in the germinal tissues shortly before the reduction division, or the meiotic divisions themselves may fail. In their case diploid gametes are formed. When fertilised by normal haploid gametes they give rise to triploids or if fertilised by another abnormal diploid gamete, tetraploids result: Alternatively, cell-division may fail soon after fertilisation, giving rise to a polyploid embryo or it may fail in somatic cells of adult plants which in some cases give rise to polyploid shoots on an otherwise diploid plant.

Until recently, it was not possible to produce polyploids experimentally; but it is now known that extremes of temperature sometimes bring about this phenomenon and more important, a substance known as colchicine produces polyploids very effectively. Colchicine is a white, water-soluble alkaloid, which is extracted from bulbs and seeds of *Colchicum autumnale* (the meadow saffron or autumn crocus). Colchicine inhibits spindle formation withou inhibiting the splitting of the chromosomes. They are unable to segregate and form a nucleus with double the number of chromosomes. Chloral hydrate has heen found to suppress one of the meiotic divisions in moses giving polyploid gametophytes, and camphor is reported to be effective with Fungi.

Polyploidy seems to have been of importance in the formation of new plant species in which self-fertilisation is usual. It has been estimated that as many as half the known angiosperms may be polyploid or derived from polyploid ancestors. *Primula kewensis* is a species which arose by the somatic doubling of the chromosomes in a hybrid between *P. floribunda* and *P. verticillata*, both of which have a diploid number of 18. The original hybrid was nearly sterile, but the tetraploid (allopolyploid) branch bore flowers which were fairly fertile on selfing. Substantiated

cases of polyploidy in animals are rare, and it is thought to be of little importance in the evolution of animal species

Finally, there is the type of alteration of chromosome number known as polysomy. Polysomics are individuals in which one or more of the chromosomes is represented three (**trisomics**) or more times. Polysomics may be derived from polyploids as well as from diploids. In *Datura*, the Jimson weed of America tetraploids are known in which one or more chromosomes are represented three, five or six times instead of the expected four times There is lilttle evidence for the existence of polysomy in animals. In *Drosophila*, individuals trisomic for the minute fourth chromosome are hardly distinguishable from normal individuals, whilst flies tetrasomic for this chromosome are inviable. No polysomics have been found among wild populations of *Drosophila*. The only established case of a naturally occurring animal trisomic is the grasshopper, *Mecostethus grossus*, in which, out of thirty individuals studied, one was found which was trisomic for the third largest chromosome.

Chromosome mutations, or simply, changes in the chromosomes, are of a gross nature, rearrangement or increase in number, compared with gene mutations which seem to be point changes. More important is the fact that chromosome mutations consist in a reshuffling or an increase in chromosome material, and hence of genes already present in the nucleus, whereas gene mutation is a change presumably in the chemical properties of a minute amount of the chromosome meterial. The position-effect phenomenon, however, suggests that gene mutations and chromosomal changes are not necessarily as fundamentally distinct as they might apear to be at first sight.

I. The Species Concept.

Classification is possible because discontinuities do exist between varying series of organisms. The limits of the various discontinuous groups on the higher levels are rather easily ascertained, although the rank and relationships of a particular group may be disputed. Thus the Onichophora are treated by some systematists as a class of Annelida, by others as a class of Arthrapoda, and by still others as an independent phylum. Some even unite all three groups in a single phylum Articulata. But advocates of all these ideas agree as to which animal are Onichophorans and which are not. Again, a group treated as an order with several families by a 'Splitter' may be treated as a single family by a 'lumper', while both men agree on what genera Comprise the group. To the extent that discribed groups correspond to such actually discontinuous groups in nature, and that is generally the case, the conventional classifications may be said to be natural. But to the extent that the rank accorded the various groups is arbitrary, the system of classification itself is arbitrary rather than natural. Taxonomists generally are agreed that while the discontinuities of the higher groups are real their asignment to systematic catagories is primarily a matter of convenience. Linnaeus himself said this is of the higher catagories, but the species he regarded as a real thing, each one a specially created unit. The replacement of the archetypal concept with the evolutionary concept has not been accompanied by an abandonment of Linnaeus idea of the definiteness of species. As Bateson has said "Though we cannot strictly define species they yet have properties which varieties have not and the distinction is not merely a matter of degree.

It becomes obligatory then to discuss the nature of this unique Taxonomic unit, the species. The species were defined as kinds of plants or animals, the individual of which differ from each other only in

minor traits except sex, sharply separated in some traits from all other species and mutually fertile, but atleast partially sterile when crossed to other species".

2. What Keeps Species Distinct?

The division of a single population in to two parts, which subsequently evolve in to distinct species, is possible only if there is some barrier to interbreeding. In the early stages of divergence it seems likely that geographical isolation is the commonest type of barrier, although it was suggested that in the case of 'biological races', environmentally caused differences in Physiology and behaviour can favour the evolutionary divergence of two populations inhabiting the same area.

Several examples were given of populations which, although they probably first diverged when spatially isolated from one another have subsequently expanded their ranges, so that today they live side by side in the same regions without loosing their separate identities. Some of the processes are whereby two related populations inhab iting the same geographical region can remain distinct. Such processes have been called by Dobzhansky 'isolating mechanisms.' The essential feature of such mechanisms is that they shall prevent, or greatly reduce, the exchange of genetic material between two populations; in the absence of such mechanisms the two populations will merge in to a single interbreeding unit, as appears to be happening at the present time to our own species.

One of the Chief methods of studying such isolating mechanisms is to hybridize different varieties and species. It is convenient to start with a classification of isolating mechanisms; such a classification has been suggested by Dobzhansky, whose ideas are accepted with slight modifications in the following scheme.

I. Geographical or Spatial Isolation.

(Space)

II. Barriers Preventing the Formation of Hybrids :—

(A) Isolation by habitat -

(B) Seasonal isolation

(C) Lack of mutual attraction between males and females of different species of animals.

(D) Mechanical isolation, physical non-correspondence between the genitalia or floral parts.

(E) Prevention of fertilization.

III. Hybrid Inviablity :—

First generation hybrids are formed but either they do not survive at all or survive poorly in competition with the parental types.

IV. Hybrid Infertility :—

First generation hybrids fail to produce functional sex cells.

V. Hybrid Break down :—

First generation hybrids viable and fertile, but later generations weak or unfertile.

Any one of these processes acting by itself could be sufficient to prevent the merging of two populations Usually however, several are found to be operating in any given case, although one may be of major importance in the wild... There are a few cases known in which two species, which in nature are found in two different geographical areas are not separated by any other mechanisms if they are brought together in the same place. For example, if the Bluewinged Teal (Anas discors) and the cinnamon Teal (Anas eyanoptera) are kept together they interbreed freely, producing fertile hybrids and forming in time a single mixed population.

Sexual Selection

A second special feature of Darwin's theory, that of sexual selection, has fared even less enviably than has that of adaptive resemblances. Darwin believed that the general theory of natural selection could not account for the colour differences which so commonly characterise the sexes, nor for other types of ornamentation differentiating the sexes. He therefore proposed the theory of sexual selection to account for such differences. In brief the the theory is that the female selects her mate and that therefore any male which is especially attractive will have improved chances of obtaining a mate and leaving descendants. This leads to development, in the male, of brilliant colors, elaborate combs, ornamentative looks, in fact, of any secondary sex character which might be regarded as potentially atractive. Darwin included also antlers, tusks, and spines which, however, could also be accounted for by the general theory of natural slection.

The idea of sexual selection requires either that males be more numerous than females, or that polygamy be the rule; that the ornamentation of the males be attractive to the females, and that the females select their mates. Some positive evidence in favour of the theory has been obtained, but it is very scant. Generally speaking the numbers of males and females seem to be about equal. There is some outstanding examples of polygamous societies among animals. One of the best is the fur seal, which breeds on the Pribilof Islands near Alaska. The males arrive at the breeding grounds before the females and engage in mortal combat most of the males are either killed or driven from the breeding grounds. Upon arrival of the females each surving male has an extensive 'harem'. Another fact which has been interpreted as supporting the theory concern those instances in

which there is a reversal of the usual pattern of sex, behaviour, for e g, phalaropes (a kind of sandpiper are characterized by brilliant plumage in the female and dull plumage in the male. But the female does the courting, while the male builds the nest and incubates the eggs.

There is much doubt how much influence ornamentation may have upon actual selection of mates. The male seals have powerful tusks but the female do not appear to have any choice of mates; they simply accept the male which is at hand when they arrive on the breeding grounds. In some cases secondary sex charactess appear to excite sexual activity without actually influencing choice of mates. In drosophila mating is preceded by court-ship behaviour which includes wing movements by the male. Wingles males can mate with normal females, but it takes much longer. Now Sturtevant has shown that if a normal pair is put in to a bottle along with a wingless male, the female will mate after a normal time lapse, but she will mate with the wingless male as with the normal one. It is evident that the court-ship of the normal male has hastened receptiveness of the female without influencing her choice of mates.

Finally, most attempts to determine factors in choice of mates have been inconclusive. It may well be the court-ship behaviour in general has more to do with sexual excitement than with choice of mates. And it may well be that simple proximity has more influence on choice of mates than does any other factor for most animals. As the problem of sexual selection now stands then probably few biologists would care to state categorically that it plays no role in evolution, but equally few would care to ascribe to it a really important role.

Orthogenesis.

Of the several hypothests to account for the origin of species which are opposed or supplemental to the Darwinian factor of natural selection, two stand out sharply as of great importance, if they are finally found to be ture. At present the mass of evidence which can be offered in favour of each is to some extent nullified by other well attested facts, and so the matter stands sub-judice. Of these hypothesis that of *orthogenesis* stands first, although it is not an explanation of evolution but a statement of possible fact.

Orthogensis (ortho=straight, genesis=production) It is the assumption that variations and hence evolutionary change occur along certain definite lines impelled by laws of which we know not the cause. Thomson says of it: "we must be on our guard however against the possible fallacy of concluding from the apparent orthogenesis in fossilised and surviving stages that there was no zigzagness and pruning in the proces. Types may have had their waywardness gradually sifted out of them."

Orthogenesis has been proposed in explanation of several phenomena for which natural selection seemingly cannot account, such as: 1. The beginings of advantageous modifications by the selection of the individual variations occurring in every direction of change, for it is evident that unless a character appeared atonce in a degree of development to give it "selection value", it would be difficult to account for its begining. But the teachings of the Neo Darwinians postulate the selection of minute random variations as well as such saltations as the idea just stated would imply.

2. Disadvantageous structures or degrees of development, such as structures which have apparently evolved along fixed and seemingly not advantageous

lines, and the development of parts beyond the point of greatest usefulness, even so far as to lead to individual death or racial extinction. Paleontology reveals to us repeated in stances of the evolution of characters which lead on to extinction, such as the huge unwieldy size of the sauropod dinosaurs the growth of excrescences, observed in the armoured and horned dinosaurs and later in the Irish deer: all of which are examples of development along disadvantageous lines or to disadvantageous degrees. Natural selection implies racial improvement, and the development of advantageous and not detrimental structurers; hence the theory of orthogenesis has been proposed to account for the latter as well as the former.

3. Degeneracy and the loss of structures. As we have seen the reversal of natural selection would account for the elimination of a character formerly useful, but which in altered circumstances has become a positive manace to survival. On the other hand if the structure becomes merely valueless, cessation of selection would account for it's diminution but not it's utter elimination. Orthogenesis has been offered as a supplementary explanation here.

Explanations of orthogenesis

The two principal explanations of orthogenesis have been stated by Newman. " Carl Von Naegeli's ideas ....involve a relief in a sort of mystical principle of progressive development, a somthing quite intangible; that exists in organic nature, which causes each organism to strive for or atleast make for specialisation or perfect adaptation........ Naegeli beleived that animals and plants would develop essentially as thay have without any struggle for existence or natural selection. Hence this form of orthogenesis theory is.........alternative to natural selection."

Thedore Eimer's explanation is more scientific and less mystical than Naegeli's. " He believed that lines

of evolution were not miscellaneous and haphazard but were confined to a few definite directions, determined at their initial stages not by the inheritance of acquired characters. A new character makes its begining as would the first step in a slow chemical change or series of such changes, and it must go through to a fixed end, under given conditions, just as surely as does the chemical process. The causes of orthogenesis are said "to be in the effects of external influences, climate, nutrition or the given constitution of an organism." Natural Selection is therefore subordinate but not dismissed.

Orthogenesis Contrasted with Ortho-Selection

At first sight there seems, to be no real, distinction between orthogenesis and decent controlled by selection as the latter must also lead to evolution along certain definite lines, in fact it can produce no other kind of evolution. Where modification is the result of the elimination, through the selective struggle, of all other lines of variation, it may be called ortho-selection. In orthogenesis how ever the lines of variation are presumed to be pre determined; hence the resultant lines of evolution are also.

Positive Evidences for Orthogenesis

1. **Parallelisms:**—Analogous or parallell variations are of frequent observation. They are the modifications of similar character which appear in different branches of the same large group or in unrelated groups, although in the later case they are often called convergences Comparative anatomy has revealed many examples to show that modifications in a definite or determinate direction may be seen in all the subgroups of a large family although appearing in varying degree in different species. Examples are the total reduction of side toes among the artiodactyles which has occurred in several unrelated gerera such as the giraffe, camel, and prong-buck. A still more remark-

able instance would be the parallelism which existed between the pseudo-horses of S. America and the true-horses of the northern hemisphere. In this instance the relationship is quite remote although in both cases the races belong to the ungulate group.

2. **Over—Specializations.** These are the numerous "excessive structures" which are developed far beyond the limits of usefulness. Such for dxample, are the tusks of the wild hog (Bahirusa alturus), the huge horns of the 'big horn' sheep, or the enormously elongated and slender neck of several weevil—or snout—beetles like Apoderus. One of the dolphins, Mesoplodon, has a mouth which can be opened but a little way when the animal is full grown, because a lower tooth grows around the upper jaw on either side. Such excessive structures which have probably contributed to the extinction of many former species, include among others the tusks of the Jefferson mammoth and the antlers of Irish deer.

3. **Constitutional Limitations on Variation.**

The constitution of the body permits as a rule, changes only in a few directions. The breeder of animals or plants may not always produce any desired form or colour. No one has yet succeeded in producing a blue *Maillbume,* a grass with divided leaves, a hen with a parrot's beak. And we can be confident that a notochord can never appear in a beetle. In this connection it should be mentioned that some biologists have seen in this restriction in the range of variation which inevitably accompanies specialization an important factor in the determination of lines of descent.

4. The correlations which bind each organ to others also restrict the range of variation.

5. **Facts from Paleontology Supporting Orthogenesis.** Many facts of paleontology seem to prove the existence of orthogenetic evolution. Wherever

sufficient material permits the working out of a phyletic Series, we always see a comparatively limited number of lines of development which, except for occasional lateral branches, run essentially in Straight lines in gradational steps. The cusps of teeth in the mammals afford interesting instances or orthogenesis as they emerge complete and do not depend upon use for their production, infact use destroys rather than perfects them, yet they appear independently but always in the adaptive position in many orders of mammalia. From observing the initial trend the ultimate tooth pattern may be often accurately predicted.

Osborn's exhaustive study of the titanotheres, a group of huge Tertiary perissodactyls has led to many generalisations.

"The phyletic series......of recent species also show where we are able to trace them distinctive single lines of development" (Kellogg.)

Kinetogenesis

Cope's theory of Kinetogenesis or "mechanical genesis" has been accepted so widely, especially by paleontologists and pathologists, that it should be studied in some detail, with the vital objections which have been raised against it.

The word *Kinetogenesis* is thus defined: The doctrine or hypothesis that animal structures have been produced directly or indirectly, by animal movements." Cope's arguments, especially as applied to the Vertebrates, are based upon the following: The Vertebrates present two distinct advantages. First, we have a more complete palentologic series. Second, we have the best opportunity for obsevation and experiment on their growth processes, since we ourselves and companions of the domesticated animals belong to this branch of the animal kingdom.

Cope and others have taken many instances such as the modification of form in to radial symmetry for sedentary types and bilateral for the locomotor, the mechanics of the teeth, of muscular development, of the shells of invertebrates, but enough have been given to show that numerous modifications of animals *conform* with mechanical laws whether mechanics is the prime mover in their production or not.

Objections to Kinetogenesis

several arguments have been offered by the opponents of this theory of which the most important are: First, the apparently illogical and self-contradictory assumption that stimuli of different kinds produce similar results, while stimuli of the same kind may produce different results. Experiment has proved the truth of this apparently paradoxical statement, for the irritation of bone will produce either bone deposits or bone absorption according to the degree of irritation. This moderate stimulus, such as the pressure and stretching may stimulate growth. Continued heavy pressure, on the other hand causes bone absorption at the point of contact.

A second objection which has been made to kinetogenesis is that if growth stimulus exist, how can there be a limit to increase so long as the stimulus of use prevails? This objection is met by the assumption that the stimulus is stress due to disharmony between organism and its environment, and that Kinetogenesis is the result of the effort on the part of the organisms to overcome this lack of harmony. When the organism is sufficiently adjusted to meet the requirements of the environment, equilibrium is attained, the stress is reduced to the point necessary for the maintanance of the mechanism in working condition and further growth ceases.

Despite cope's argument, this is one of the objections to his theory which is most emphasized by its

opponents. It will atonce be seen that even if the objections above are met, a third will yet remain, that of the acceptance of the Lamarckian factor of the inheritance of acquired or ontogenic modifications, upon which the whole doctrine of Kinetogenesis seems to depend for its inclusion among the potent factors of evolution.

The Germplasm Theory

Weismann (1834 — 1914), an ardent disciple of Darwin, was not convinced that pangenesis represented the true state of affairs. Consequently, he elaborated, by observation and speculation rather than by experiment, the *Germplasm Theory of Heredity*, based upon the concept that living things are made up of two kinds of materials, *Germplasm* and *Somatoplasm*, which are fundamentally different from each other in many important respects.

According to this theory somatoplasm includes the body tissues, or evident bulk of the individual that is fated in the ordinary course of events to complate a life cycle of development, growth, and death; while germplasm, on the other hand, is the immortal fragment always young, freighted with the power not only to duplicate the whole organism, but also to provide a residue which, barring accident, is destined to live on and in due time to give rise to other new individuals.

While the germplasm cells can break free from the parent organism and begin a new and independent life, the somatic cells hang together as they multiply in number to build up the tissues of the body. Weismann goes on to maintain that the excess germplasm which an individual carries along is like a "pilgrim stranger", transient guest, tarrying only for a time and hardly influenced at all by its somatic host, except possibly in a nutritive non hereditary way. Consequently it plays no direct part in the life of the individual which harbours it.

Thus, quite contrary to Darwin's theory of pangenesis, Weismann's theory affirms that germplasm is not freshly formed over and over by the body when the individual reaches sexual maturity, as it appears to be, but that it is rather a continuious substance present

from the begining and essentially immortal, although it is periodic in its activities and liable to accidental death with the death of its host.

In spite of the fact that the *Continuity of the germplasm* has been actually demonstrated in comparatively few instances, all the facts that are known concerning the behaviour of the germinal substance are consistent with this conception. The remarkably successful expriments of Carrel and others with isolated somatic tissuess, grown for years *in vitro*, suggests that potential immortality is latent even in some somatic cells as well as in the germ cells. The phrase "life everlasting," therefore, is not to be confined to the vocabulary of the theologian, for potential immortality has a demonstratable basis in biological fact and is more then a mystical hope of believing humanity.

It is to be emphasized that every organism starts out life with a marvelously small bulk of hereditary capital in the form of the fertilized egg. This wonderfull bit of germplasm is the bridge of continuity between the generations over which the hosts of inheritance must pass, and although it is always comparatively insignificant in size it may neverthe less sustain an enormous traffic.

In many of the protozoans, the entire organism is possibly comparable to germplasm, but in all forms of life that are compounded of several cells *excess germplasm* is present after the needs of the developing somatoplasm are met, and it is set aside probably early in the development of the individual, remaining undifferentiated or in reserve, while the somatoplasm is expended in forming the tissuess that make up the individual. In one instance atleast, according to *Boveri* who has followed out the cell lineage from the begining in the nematode worm *Ascaris*, this splitting off of the germplasm occurs as early in the cleavage of the fertilized eggs as the sixteen-cell stage, when

fifteen of the cells go to form the somatoplasm and the sixteenth is set aside as excess germplasm.

Thus there results a continuous stream of germplasm, receiving contributions from other germplasmal streams. From this continuous stream of germplasm there splits off at successive intervals complexes of somatoplasm or "individuals," which go so far on the road of specilization unto various tissues that the power to be "born again" is lost, and so after a time they die, while the germplasm held in reserve lives on as a continuous line in the following generations.

This explains the saying that the son, when he is deserved to resemble his father, is a "chip off the old block". The resemblance, however, is due to the fact that both father and son are chips off the *same* block. They are both somatoplasms *developing at different intervals* from the same continuous stream of germplasm, instead of the somatoplasm of the son being derived from that of the father.

As a matter of fact the germplasm from which the son arises is different from that of the father since it is modified by the addition of the maternal contribution, so that in reality the father and son hold much the same hereditary relation to each other that half-brothers do, having the ancestral hereditary stream on one side of the house in common. So far as his body, or his somatoplasm is concerned, the son is younger than his father, since he has branched from the common germ-line at a latter date, but at the same time he is older than his father with respect to his germplasm, because the continuons line of hereditary potentialities has the span of a generation longer in the son than in the parents.

From this point of view, the real mission of the somatoplasm, that is so marvelously differentiated into all the various forms called animals and plants, is

simply to serve as the temporary domicile for the immortal germ plasm which, like the Wandering Jew, is destined to reappear in successive reincarnations. Thus the parent becomes as it were the "trustee of the germplasm", but not the producer of the off spring for the soma is after all only the mechanism through which the fertilized egg in due time produces another fertilized egg. A hen is simply the device of an egg for producing another egg.

In the light of these preliminary explanations it is plain that the most hopeful point of attack in the science of Genetics must inevitably be cytological, that is, through the study of the hidden germplasm forming the genotype, which is the source or point of departure in the formation of each new individual, rather than in the consideration of the conspicuous somatoplasm or phenotype which represents only the end stages of the hereditary processes.

It must not be forgotten, moreover, that inheritance consists in more than the handing on of the continuous germplasm. In every case individuals are somatoplasms that have not only received their potentialities but have necessarily come into expression in an *environment* which has exerted a modifying influence on the developing somatoplasm The individual is always the result of the interaction of the two fundamental factors of heredity and environment, and it is rather futile to try to separate the effects of these two factors.

The reason why the attempt to do so is so often made is because such an analysis, if possible, would point the way to possible future control. For example, if a criminal is such because of bad heredity it is the plain duty of society to check the flow of the germplasm involved. If, on the other hand, the criminal becomes such because of a bad environment, is equally the obvious duty of society to change that bad environ-

ment into a better one, In either case society has a definite task to perform, but the procedure is different in the two instances. The fact that both heredity and environment must always be reckoned with makes difficult the analysis of any case that is to be followed with wise corrective interference.

The opposition to Weismann.

The opponents of Weismann point out, as a weak link in his argument, the assumption that the germplasm is so insulated from the somatoplasm as not to be influenced by it. Weismann assumes, of course, that the germplasm is isolated from the somatoplasm very early in the development of the fertilized egg into an individual, and that when once isolated it thereafter takes no part in, nor is in any way affected by the vicissitudes through which the somatoplasm, or the body itself, passes. The somatoplasm is thus merely a carrier of the germplasm and unable to affect the character of it any more than a rubber hot water-bag, although capable of assuming a variety of shapes, can affect the character of the water within it.

The possible independence of parts organically associated together as intimately as germplasm and somatoplasm, is shown also by the routine work of orchardists whose grafts never take on the character of the host tree.

Furthermore the known behaviour throughout synapsis and segregation of hereditary genes in Mendelian crosses, points unmistakably to the same possibility of close association, either nutritive or otherwise, of two different organic substances, without the one changing the character of the other thereby.

In opposition to this view it is urged that organism is a physiological as well as a morphological unity, and that cells entirely insulated within such a unity would be a Physiological miracle.

In this connection it must be remembered that nutritional dependence, without necessitating morphological modification to correspond with the course of the mutation, is a fact commonly obserevd. Feeding a baby goat's milk does not result in a kid.

There is abundant evidence that germ cells, or rather certain hormones in the organs producing the germ cells, do not affect the somatoplasm under particular conditions, as, for example, in casec of castration when those somatic features called "secondary sexual characters" undergo profound modification. Even here, however, it must he pointed out that it is not the germ cells themselves that are directly responsible for the modifications which occur, but rather the harmones of the interstitial gonadal cells.

A most serious fly in the weismann ointment is due to the results of certain experiments by Guyer and Smith.

These ingenious experiments injected into fowls the freshly removed lenses of rabbits' eyes, pulped up in Ringer's solution. The fowls developed ae "antibody" or lysin which tended to disintegrate thn rabbit lenses. When serumfrom these fowls was in turn injected into pregnant rabbits, the mother was unaffected, but nine out of sixty-one surviving young were born with degenerate eyes. The affected young carried the defect even in the male line through several generations without the injection of any more serum containing the lens antibody. "The degenerating eys are themselves, directly or indirectly, originating antibodies in the blood serum of their bearers — which in turn affect the germ cells." If these conclusions are finally substantiated, than the cardinal principle of the inheritance of acquired characters must be conceded to be possible. The end is not yet. (refer Neo-Lamarckism for objections to Weismaunism.

Variation: Heredity, or "organic resemblance based on descent", is due principally to the fact that offspring are material continuations of their parents, and conseqnently may be expected to be like them. This is not trbe always, either phenotypically or genotypically. Two brown—eyed parents; for instance, may produce a blue-eyed child, although brown - eyed children are more usual from such a parentage. It is a common experience, indeed, for breeders of plants and animals to meet with continual difficulties in getting organisms to "breed true". Nevertheless these variations which so constantly interfere with breeding true furnish the sole foothold for improvement, since if all organisms did breed strictly true, one generation could not stand on the shoulders of the preceding generation so as to make evolutionary advance possible.

Hugo Devries and Mutation

Bateson in 1894 brought together in an encyclopedic volume evidence to show that mutations, or "disconinuous variations" as he called them, were much more general than commonly supposed. It remained, however, for the *Dutch Botanist De Vries* (1848 — 1935) to attempt an analysis of the character of mutations and to focus attention upon them. There is something distinctly suggestive of the thorough and cautious method which Darwin employed in presenting his master piece, The Origin of Species, to the world in the way De Vries worked in silence for fivety years before he published 'Die Mutations theorie,' with which his name will be forever connected.

Perhaps the most historically famous of so called plant mutations have been those in the progeny of Lamarck's evening primose Oenothera Lamarckiana. It was the study of this plant that led *De Vries* to formulate his Mutation Theory.

It is known that this species was exported to London from America as an ornamental garden plant about 1860. Thence it spread to the continent where, escaping from gardens, it became wild in atlast one locality in the Neltherlands, not far from Amsterdam. Here, in an abandoned potato field, it fell under the seeing eye of De Vries in 1885, with the consequence that now both the botanist and primrose are famous.

De Vries discovered among these escaped plants not only the original Oenothera Lamarckiana, but also two other kinds which he named Oenothera brevistylis, Characterized by short-styled flowers and Oenothera laevifolia, which has smooth leaves. These were two entirely new species hitherto unknown at the great botanical clearing-houses of Paris, Leyden and the Kew Gardens in London. Since the seeds of Oenothera are ordinarily produced by self fertilized flowers, De Vries felt safe in regarding these plants as mutants rather than hybrids, and so he continued to study them with special care. Transplanting the mutants, along with representatives of Oenothera Lamarckiana, to his private gardens in Amsterdam, where it was possible to maintain them in normal healthy condition, he was able to follow their individual histories with certainty.

The wild mutants of O. laevifolia and O. brevistylis, which first attracted his attention, did not reappear under cultivation, lut he found that, out of 54,343 Oenothera Lamarckiana plants grown from nine original plants in eight years, there appeared 837 mutants, comprising seven different new elementary species, all of which bred true, with the exception of the species that he named Oenothera lata and Oenothera scintiblans. These behaved like the parent O. Lamarckiana ln producing a variety ofoffspring.

The seven new different kinds of evening primroses are distinguished from one another by features involving all parts of the plant as well as the flowers, and

are unmistakable even to the uninitiated. The systematist is amply justified in regarding them as distinct species.

De Vries' experiments and observations upon the evening primrose have since been repeated on an extensive scale, notably by Mac Dougal in the New York Botanical Gardens, by Shull of the Carnegie Institution at Cold Spring Harbour, Long Island, New York, and by Gates in England The mutability of O. Lamarkiana is as unmistakable and uniform in America and England as in Holland, and De Vries' original results and conclusions have been confirmed in all essential points.

De Vries distinguished four categories among the Oenothera mutants, the first three of which are quite likely to maintain themselves in nature. He described them as:

(1) Progressive species, due to the addition of certain characters (O. gigas, O. rubrinervis)

(2) Retrogressive species, characterized by the loss of something that was present in the parent form (O nanella, O. levifolia)

(3) Inconstant species, that do not always breed true but producc mutants.

(O. scientillans, O. lata and O. Lamarckiana)

(4) Degressive species, which are defective in some way and are probably incapable of maintaining themselves in nature (O. albida, O. oblonga)

It is somewhat questionable, however, whether this classical evening primrose, which has added atleast a five-foot shelf to the biological literature of the last few decades, is after all the most fortunate organism for demonstrating the idea of mutation. As has been pointed out by Dr. Bradley and others, it is by

no means certain that the De Vriesian mutations obtained from Oenothera Lamarckiana, although they possess the characteristic permanance in succeeding generations and so apparently fulfill the requirements for a mutation, may not after all be regarded simply as recombinations within a hybrid stock.

The term mutation has come more and more to be restricted not to recombinations but to qualitative changes in the germinal material. The fact that both qualitative changes and recombinations may breed true, makes it somswhat difficult to distinguish between them and to determine the basis of their origin.

In any event De Vries' outstanding work has stimulated biologists to be on the look out for mutations, whatever they are, with the gratifying result that instances have been abundantly forthcoming from all quarters. It is now firmly established that mutations are of general occurrence and not just occasional "sports".

Some mutations among animals:

In 1791 a Massachusetts farmer found in his flock of sheep a male lamp with a long sagging back and short bent legs, resembling somewhat a German dachshund. With unusual foresight he carefully brought up this strange lamb because it was an animal that could not jump fences. It occurred to this hard-headed Yankee that it would be much easier to get together a flock of short low legged sheep, unable to negotiate anything but a low hurdle, than to labour hard in building high fences. So it came about that this mutant lamb, in the hands of a man who appriciated lobour-saving devices, became the ancestor of the famous Ancon breed of sheep. Later this breed gave place in public favour to the merino, probably also a mutant, which produces a superior grade of wool.

Some mutations, like albinism, that may be selected and maintained by man, unlikely to succeed in nature when left to their own divices. Albino rats, set free by Dr. Hatai some years ago upon a small uninhabited Island in Long Island Sound, all shortly succumbed in competition with native gray rats. Albinism is a mutation which has appeared not only in man himself and many domestic animals, such as rabbits, rats, mice, and guinea pigs, but also in foxes,, skunks, squirrels, birds and insects.

Additional mutants among the animals may be cited as follows; multi-nippled sheep, double-eared cattle, silky fowls, pacing horses, polydactylous cats and mule-footed swine. Davenport writing of his experiments in breeding poultry, says, "During the past four years I have handled and described over 10,000 poultry of known ancestry. Of striking new characters I have observed many, some incompatible with normal existance, others in no way unfitting the individual for continued life. In the egg inhatched I have obtained Siamese twins, pug jaws, (snubbed nose) and chicks with thigh bones absent. There have been reared chicks with toes grown together with a web, without toe nails or with toenails two to a toe; with five, six, seven, or three toes; with one wing or both lacking; with two pairs of spurs; without oil-gland or tail, with neck devoid of feathers; with cerebral hernia and a great crest; with feather shaft recurved, with barbs twisted and dichotomously branched or lacking altogether. Of comb alone I have a score of forms. All these characters have been offered to me without the least effort or conscious selection on my part, and each appeared in the first generation as well developed peculiarities, and in so far as their inheritance was witnessed each refused to blend when mated with a dissimilar form".

The chief reason why definite examples of mutation have been so infrequently noted and recorded is

because the attention of the investigator has generally been directed not to them but to the gradual fluctuating quantitative variations which, according to Darwin's conception, furnish the principal materials for the operations of natural selection. Mutations are doubtless much more common than has been generally supposed. Their apparent scarcity in nature is largely due to the lack of critical examination. Drosophila, is a good example of many deviations of a mutational nature that have been reveealed upon carrful and persistent scrutiny. Upwards of a thousand different mutations have been reported for this glnus alone, but over forty million flies have been critically examined by different investigators in attaining this remarkable result.

Three kinds of Mutations: There seems to be no reason why mutation may not occur at any stage in the life cycle of an organism. Thus, in origin a mutation may be gametic, Zygotic or Somatic.

Gametes are the ripe germ cells which unite to form the fertilized egg, or Zygote. It is obviuos that a gametic mutation usually enters the organism concerned singly, that is, from one parent only, and if it becomes covered up by the corresponding character from the other parent, it will fail to put in an appeanance immediately in the developing somatoplasm. It may be carried on concealed for many generations. If, however, the mutation comes from both parents, or is of sufficient intensity from one parent to show in spite of what the other parent contributes, it will make itself known at once.

Zygotic mutations occur after the union of germ cells in the fertilized egg, and consequently appear immediately in the developing individual.

In contrast to the two kinds of mutations which are distinctly germinal in origin, a Somatic mutation

falls directly upon some individual somatic cell or tissue arising out of the original germplasm, and becomes evident in all the cells and tissues that subsequently are derived from it. In such cases all the cells and tissues arising from the mutant cell, *and no others*, will express the mutation. This type is especially common in plants, and furnishes such abnormalities as bud variations, chimaeras, and the like, all of which can only be propagated asexually by grafts or cuttings.

A Chimaera is the result of two diverse tissues growing together in intimate contact like Siamese twins, each retaining itsown original character immodified by the other. For Example, when a scion or twig from a pear tree is grafted upon the limb of an apple tree, both pears and apples may be produced on separate limbs of the same tree. If now adventitious buds sprout out from the regin where the graft joins the original tree, they may contain cells from both sources and form a limb on one side of which pears are produced and on the other side apples. Such a mined limb is a typical artificial Chimaera.

Distribution of Species

Introduction. From the time of LINNAEUS, biogeography was a very active field in which many of the most distinguished biologists worked. New phyla were described fairly frequently, new classes and orders with regularity. By the end of the 19th century all of the major biogeographical realms were fairly well known. The development of geographic isolation between related populations is certainly an important aspect of biogeography.

Island Life. It was the study of the flora and fauna of the Galapagos Islands that first caused Darwin to consider the possibility that species might be mutable and the island life of the Malay Archipelago played a

major role in bringing Wallace to the same conclusion. Many features inherent in the island combine to cause this. The fact that the inhabitants of any island generally resemble those of the nearest main land leaves little doubt that the island dwellers have migrated from the mainland. However unless an island is very close to the main land, there are the difficulties of crossing the water barrier which keep out a portion of the potential migrants. Thus competition is less vigorous and often in the absence of predators the population may reach prodigious numbers relative to the space available. In such a situation, genetic drift may be stronger than selection, with the result that island form are likely to be less well adopted than their main land relatives. Apparently contradictory to this is the fact that closely related island dwellers may become adapted to situations so different that only remotely related organisms of the main land could be compared to them.

Rapid selective Differentiation on Oceanic Islands. One of Darwin's studies in the Galapagos islands was made upon a family of finches the Geospigidae. Another family of birds the Drepaniidae or Hawaiin honey creepers has undergone on similar adaptive radition within a geologically brief time. The Hawaii Islands appear to have originated no earlier than the Pliocene As the honey creepers are forest dewellers, their original ancestor could not have reached Hawaii, (by migrating from Central America) before the forests themselves were established. This might have occurred by mid pliocene or later than giving a maximum of 5 million years for the differentiation of the family in Hawaii.

When the remote ancestor of the Drepaniidae first migrated from the main land to the Hawaiian forests, it found a rich field for which it had no competitors. The result was a rapidly expanding population which soon provided its own competition. That is the population began to outstrip the food supply available by the original method of feeding.

Endemism. Closely related to the phenomena sland life is that of endemism. Endemic is defined a estricted to or prevalent in a particular district. Thus efined, all species are endemic for all are confined to a efinite area, even though the area may be very great. Two different types of endemic species are recognised. A pecies may have a very restricted distributions because t is a young species. Or a species may have a restricted range. Some biologists reserve the term endemic for the first type, while calling the second epibiotic. Yet most species of restricted distribution fall in to the latter class.

Island life, particularly that of oceanic islands is replete with endemics. It has been estimated that more than 90 per cent of the flora of the Hawaiian islands is endemic. The high proportion of endemics in the Galapagos islands was among the factors which directed Darwin's thought towards the possibility of the transformation of species.

Darwin's Pangenesis Theory.

Darwin realized his doctrine of natural selection lacked completion if he merely accepted the fact of heredity at its face value without trying to learn in what way mental or physical traits of new variations got into the egg or sperm and thus were borne on to the next generation. He therefore devised the theory of pangenesis, according to which every cell of every tissue and organ of the entire body produces minute particles called gemmules, which in each instance part take of the nature of the cells producing them. These gemmules may circulate throughout the entire organism but finally congregate in the reproductive products or in buds, so that each germ cell or each bud (asexual) capable of giving rise to a new individual would be in a sense a miniature replica of the parents' body and would thus be capable of developing into the same kind of a body even in minute detail. Darwin thought that sometimes certain of the gemmules might be dormant for several generations

d then develop, bring out in an individual it ancestral (atavistic) traits.

If this theory of gemmules were true it would lead t the acceptance of the teaching of Lamarck or even o Buffon, because under such circumstances the inheritance of acquired characters gained by the parent during its life time would be entirely feasible, for such modification could be impressed upon the germ cell as readily as could the variations which we call germinal.

Later research, however proved that such a theory has no basis in fact and biologists soon began to search for a substance which could be a physical basis of heredity, just as the protoplasm which makes up the bulk of all organisms is the physical basis of life, and while several biologists were convinced that there was such a substance it remained for August Weismann, for nearly fifty years professor in the university of Fraburg to identify and demonstrate its existence.